THE ROLE OF WATER CLARITY IN STRUCTURING NICHE DIMENSIONS AND OVERLAP BETWEEN SMALLMOUTH BASS AND WALLEYE

by

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ABSTRACT

Smallmouth bass (*Micropterus dolomieu*) have experienced substantial range expansions in northern Ontario over the past century, with adverse consequences for native salmonid predators. It is unclear how climate-induced water clarity shifts will affect interactions between native dark-adapted walleye (*Sander virteus*) and invading smallmouth bass in northern Ontario. This study used stable isotopes of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) in fish muscle tissue to investigate how resource partitioning between walleye and smallmouth bass is related to water clarity in 34 small (100-200 ha) Boreal Shield lakes (ranging from 1 to 8.5 m Secchi depth, and from 3.2 to 13.1 mg/L DOC). Quantitative metrics of trophic niche dimensions (based on the size, position, and dispersion of multivariate ellipses drawn around sampled individuals in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space) were calculated for each individual population and used to determine trophic interactions and niche overlap between sympatric walleye and smallmouth bass. Linear and multiple regressions were then used to explore potential relationships between trophic interactions and water clarity. Available habitat and fish assemblage data was also explored for potential influences on isotopic niche dimensions and trophic interactions of walleye and smallmouth bass. Total occupied niche space decreased significantly with increasing water clarity for smallmouth bass as populations occupied a narrower range of trophic levels and made greater use of pelagic resources. In contrast, walleye trophic niche dimensions did not respond significantly to water clarity. Isotopic niche overlap ranged from 0 to 65%, but no metric of trophic overlap was significantly related to water clarity. Other abiotic and biotic variables, however, did have a significant influence on the similarity between some aspects of walleye and smallmouth

bass isotopic niche dimensions (but not interaction). Both species fed on more isotopically similar carbon sources as lakes became shallower, which may be a result of a lack of distinct littoral and limnetic habitats. Walleye and smallmouth bass niche size also became more similar with increasing DOC but this may be a result of lower prey diversity. Both species also occupied more similar average food web positions as yellow perch relative abundance increased, indicating that the exploitation of yellow perch by both species increased with perch abundance. Together with other studies that have found little evidence for an impact of smallmouth bass on walleye fitness and abundance, this research suggests that, unlike salmonid and cyprinid species, walleye may be resilient against smallmouth bass invasions regardless of water clarity conditions in oligotrophic boreal lakes.

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INTRODUCTION

Invasive species can severely alter food webs and detrimentally impact native communities (Lodge 1993). Invasive species are commonly perceived as foreign invaders from distant geographical regions or vastly different ecosystems, while the dispersal of species from nearby ecosystems is considered less threatening. Smallmouth bass (*Micropterus dolomieu*) is one exception to this perspective. Native to the Laurentian Great Lakes and St. Lawrence River basins, the species range in North America has greatly expanded over the past century (Scott and Crossman 1973; Sharma and Jackson 2008), sparking concerns among fisheries managers in Canada and the northern United States regarding impacts on native fish assemblages (DFO 2009; Neuswanger 2009; DFO 2011; Funnell 2012). Although smallmouth bass are native to Ontario's north-temperate lakes and have been known to co-exist in southern lakes with many of the native boreal predators, smallmouth bass introductions into Boreal Shield lakes of northern Ontario have been associated with major population declines of lake trout (*Salvelinus namaycush;* e.g., Vander Zanden et al. 1999), brook trout (*Salvelinus fontinalis;* e.g,. Brown et al. 2000), and cyprinid species (e.g., Jackson and Mandrak 2002). Smallmouth bass are efficient littoral predators that can quickly reduce prey fish abundance upon introduction (Jackson and Mandrak 2002), forcing native pelagic predators such as lake trout to rely more heavily on less energetically-profitable forage (Vander Zanden et al. 1999). They also pose a challenge to littoral brook trout, which are thought to be poor competitors for shared fish and invertebrate prey (Bourke et al. 1999). Indeed, brook trout are rarely found in sympatry with smallmouth bass (Jackson 2002). Legal bass stocking in Ontario ended in the 1980's as evidence for adverse impacts gathered (Kerr 2006), but

smallmouth bass introductions have continued through unintentional bait bucket releases, illegal transfers by anglers, and natural movements through stream connections (reviewed in Funnell 2012). Range expansion has also been aided by greater overwinter survival and production at the northern edge of the range as the climate warms (Shuter and Post 1990).

Recent anecdotal evidence from anglers in the northern United States suggested that stocked smallmouth bass were also causing declines in established walleye (*Sander vitreus*) populations (Wuellner 2009; AFS 2010). Walleye is the most important recreational, commercial, and subsistence fish in Ontario (Rietveld et al. 1999) and is also economically valuable in the northern United States, making it a focus of management and stocking programs. Reported walleye declines thus prompted a flurry of studies in the northern U.S. to understand walleye-smallmouth bass interactions (e.g., Fayram et al. 2005; Wuellner et al. 2010; Galster et al. 2012). Studies generally found little evidence for negative impacts of smallmouth bass on walleye, although the degree of reported competition was variable. None of these studies were conducted in lakes on the Boreal Shield, where the majority of salmonid and cyprinid declines were reported, and little attention was given to water clarity conditions despite the known importance of visual acuity to hunting for both predators (e.g., Ryder 1977; Skewa and Hartman 2003).

Lakes in Ontario's Boreal Shield region are biologically and limnologically distinct from the American study lakes (Vander Zanden et al. 1999; Vander Zanden et al. 2004; Lepak et al. 2006; Kaufman et al. 2009). Firstly, the boreal landscape is dominated by small, oligotrophic lakes (estimated 98% between 1 and 100 ha; Cox 1978). Smallmouth bass are more successful at dominating the littoral zones in smaller lakes than in large lakes (Funnell 2012). Secondly, many of the recent studies were conducted in lakes with concurrent walleye and bass stocking programs (e.g., Fayram et al. 2005;

Wuellner et al. 2011; Galster et al. 2012), whereas lake trout declines from smallmouth bass invasions were often found in "remote" boreal lakes with no history of stocking (Kaufman et al. 2009). Thirdly, water clarity conditions in boreal lakes vary widely across the landscape from very dark (< 1 m Secchi depth) to very clear (> 10 m Secchi depth), which could have important consequences for interactions between smallmouth bass and walleye.

Both walleye and smallmouth bass are visual piscivores, yet an important distinction may affect their position and influence within boreal food webs. The visual acuity of smallmouth bass is greatest when subsurface illumination is high (Skewa and Hartman 2003; Carter et al. 2010), and they are most commonly associated with clear waters where they hunt primarily during daylight hours (Scott and Crossman 1973). In contrast, walleye have specialized eye structures adapted for foraging in dark waters (Ali et al. 1977). Walleye hunt most actively during crepuscular periods and through the night (Ryder and Kerr 1978), often following shoaling prey fish such as yellow perch (*Perca flavescens*) into nearshore habitats (Ryder 1977; Ali et al. 1977). In darker waters walleye are active throughout the day, consequently lowering the incidence of crepuscular feeding, especially if pelagic forage fish such as rainbow smelt (*Osmerus mordax*) or cisco (*Coregonus artedi*) are available (Jones et al. 1994; Henderson et al. 2004).Water clarity is thus an important influence on foraging behaviour. Walleye retinas also contain two forms of cones: midwave and longwave that have maximum sensitivity at light wavelengths of 533 nm and 605 nm, respectively (Burkhardt and Hassin 1983). This coincides with the spectral composition of waters stained by dissolved organic carbon (DOC), which often narrows the spectral composition of penetrating light to wavelengths

of 500 to 600 nm and imparts a distinctive brownish-yellow colour to humic waters (Pitcher 1993).

DOC is the primary determinant of water clarity in small (< 500 ha), oligotrophic lakes in the boreal forest (Fee et al. 1996; Keller et al. 2006). DOC concentrations are expected to increase in lakes across the boreal forest biome as a result of climate warming and reductions in anthropogenic acidification (Miettinen et al. 2005; Benoy et al. 2007; Monteith et al. 2007), with potentially important consequences for north-temperate fish communities (Appendix A). Altered visual light environments have been shown to play a key role in shifting the competitive balance between other visual piscivores. For instance, arctic char (*Salvelinus alpinus*) are stronger competitors than sympatric brown trout (*Salmo trutta*) in dark waters while brown trout dominate in clear waters (Helland et al. 2011). This results in cohabitation of the littoral zone under the cover of ice, and a higher impact of arctic char on brown trout consumption rates in winter and in dark lakes (Ulvan et al. 2012). A similar relationship between walleye and smallmouth bass could be responsible for the lack of evident competitive relationships found in previous studies, given the strong dependency of both species on visual acuity for hunting, and their opposite phototaxis. Darker waters created by enhanced DOC loadings under climate change could confer an advantage to walleye over smallmouth bass. Conversely, clear lakes may require more intense management strategies than dark lakes to offset potential competition with smallmouth bass.

The first condition for inter-specific competition is that two species share resources (Birch 1957). Here, I use natural abundance stable isotopes in fish muscle tissue to infer walleye and smallmouth diets and thereby assess the potential for competition under varying light regimes. The heavy isotope of nitrogen (^{15}N) becomes enriched

relative to the lighter isotope (^{14}N) at higher positions in the food chain, largely due to greater excretion of the light isotope in urine (Steele and Daniel 1978). The exact mechanism for this biased excretion is not well understood, although it most likely occurs during the process of protein elimination from the body such as through discrimination against the heavy isotope during urea synthesis (Schoeller 1999). The ratio of $^{15}N/^{14}N$ in consumer tissue (often reported as $\delta^{15}N$) can thus be used as an index of trophic level (Cabana and Rasmussen 1996). Isotope enrichment rates up the food chain are minimal for carbon (Rounick and Winterbourn 1986), but the rates of ^{13}C vs. ^{12}C accumulation are distinct between pelagic and benthic primary producers in aquatic systems (France 1995). Benthic algae grow in a relatively stagnant boundary layer near the bottom whereas pelagic algae grow in the more turbulent water column. Because dissolved CO_2 is often more limiting in the former habitat, benthic algae utilize a higher proportion of the heavier and less preferred $^{13}CO_2$ and have a more positive $^{13}C/^{12}C$ ($\delta^{13}C$) "signature" than pelagic algae (France 1995). These $\delta^{13}C$ signatures are conserved at higher trophic levels and provide an indication of the habitat from which a consumer ultimately derives its energy.

The dispersion of individuals in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space can be used to create proxies for a population's realized dietary niche dimensions (Bearhop et al. 2004). Here I used variation ellipses expanded to quantify isotopic niche dimensions of sympatric populations of walleye and smallmouth bass, along with their dietary overlap, in oligotrophic boreal lakes that span a wide gradient of water clarity. I then used several metrics adapted from Layman et al. (2007) and Jackson et al. (2011) to quantify trophic interactions between species based on dispersion in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space, and provide supplemental code for calculating modified metrics in the R statistical package.

Specifically, I hypothesized that (1) smallmouth bass niche dimensions will contract with increasing water clarity because individuals are able to feed more efficiently on preferred prey items (thereby reducing within-population variability in isotope signatures), (2) walleye niche dimensions will expand with increasing water clarity because less favourable light conditions will result in greater opportunistic feeding (thereby increasing within-population variability in isotope signatures), and (3) isotopic niche overlap will increase with water clarity as walleye must make greater use of crepuscular feeding on shoaling prey fish, and as smallmouth bass are able to expand foraging into well-lit pelagic habitats (Figure 1). Although I was primarily interested in water clarity, I took advantage of available lake chemistry, morphometry, and fish assemblage data to investigate other potential habitat (Figure 2) and fish community (Figure 3) variables that could explain a portion of the variation in isotopic niche dimensions and dietary overlap between native walleye and invasive smallmouth bass.

METHODS

Study Sites and Sampling

Thirty-four lakes that spanned a gradient of water clarity (from 1 to 8.5 m Secchi depth, and from 3.2 to 13.1 mg/L DOC) were selected across the Boreal Shield in Central, Northwestern, and Northeastern Ontario (Figure 4, Table 1). Study lakes had surface areas between 73 and 196 ha, were considered oligotrophic ([total P] < 0.04 mg/L; Wetzel 2001), and were located within a relatively narrow climatic gradient (from 1430 to 1860 GDD > 5 °C). Twenty-eight study lakes contained both walleye and smallmouth bass, but to infer whether isotopic niche dimensions were affected by contact between the two

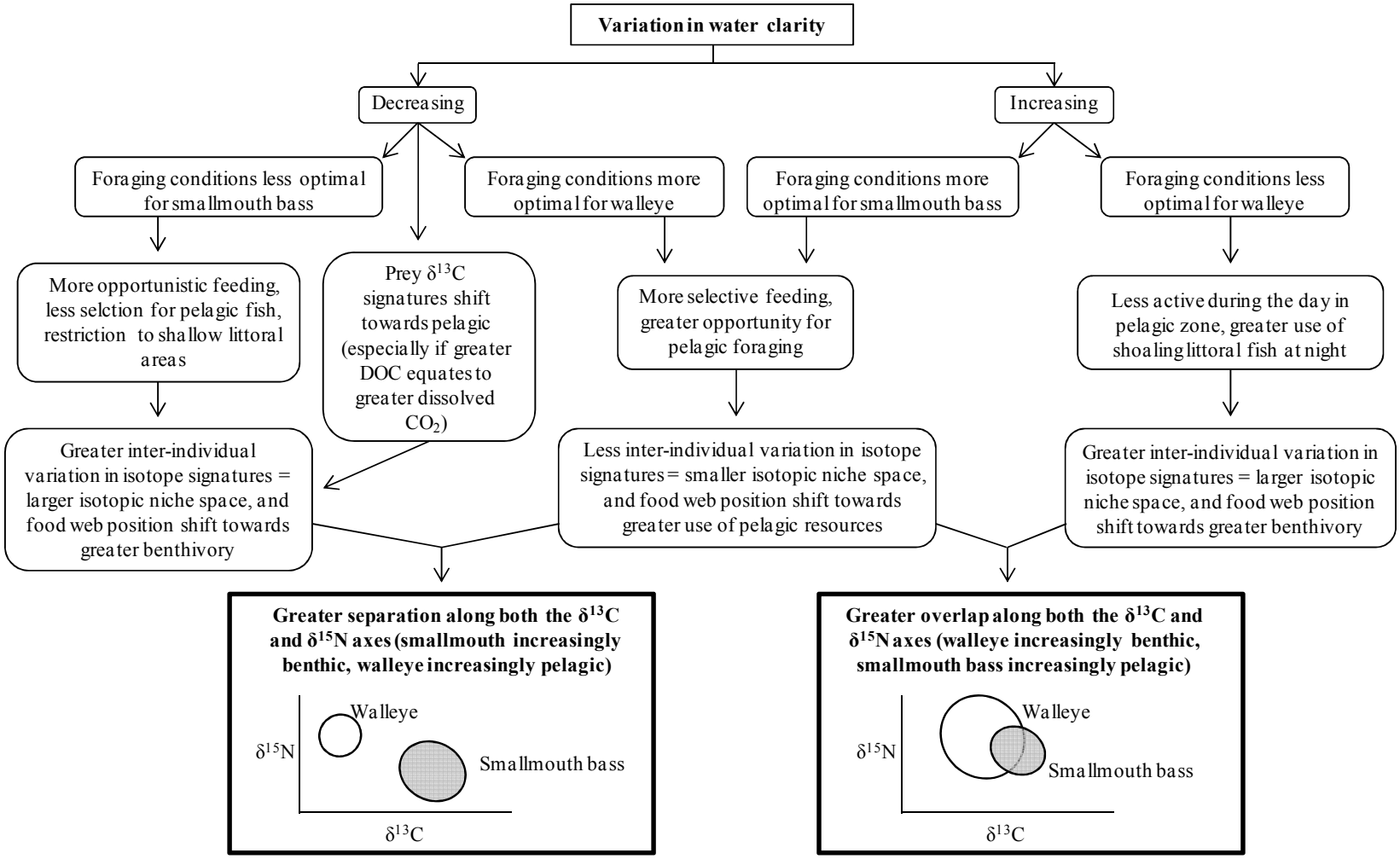

Figure 1. Conceptual diagram of hypothesized responses of walleye and smallmouth bass feeding behaviour, isotopic niche dimensions, and isotopic niche overlap to changes in water clarity, if all other variables were held constant.

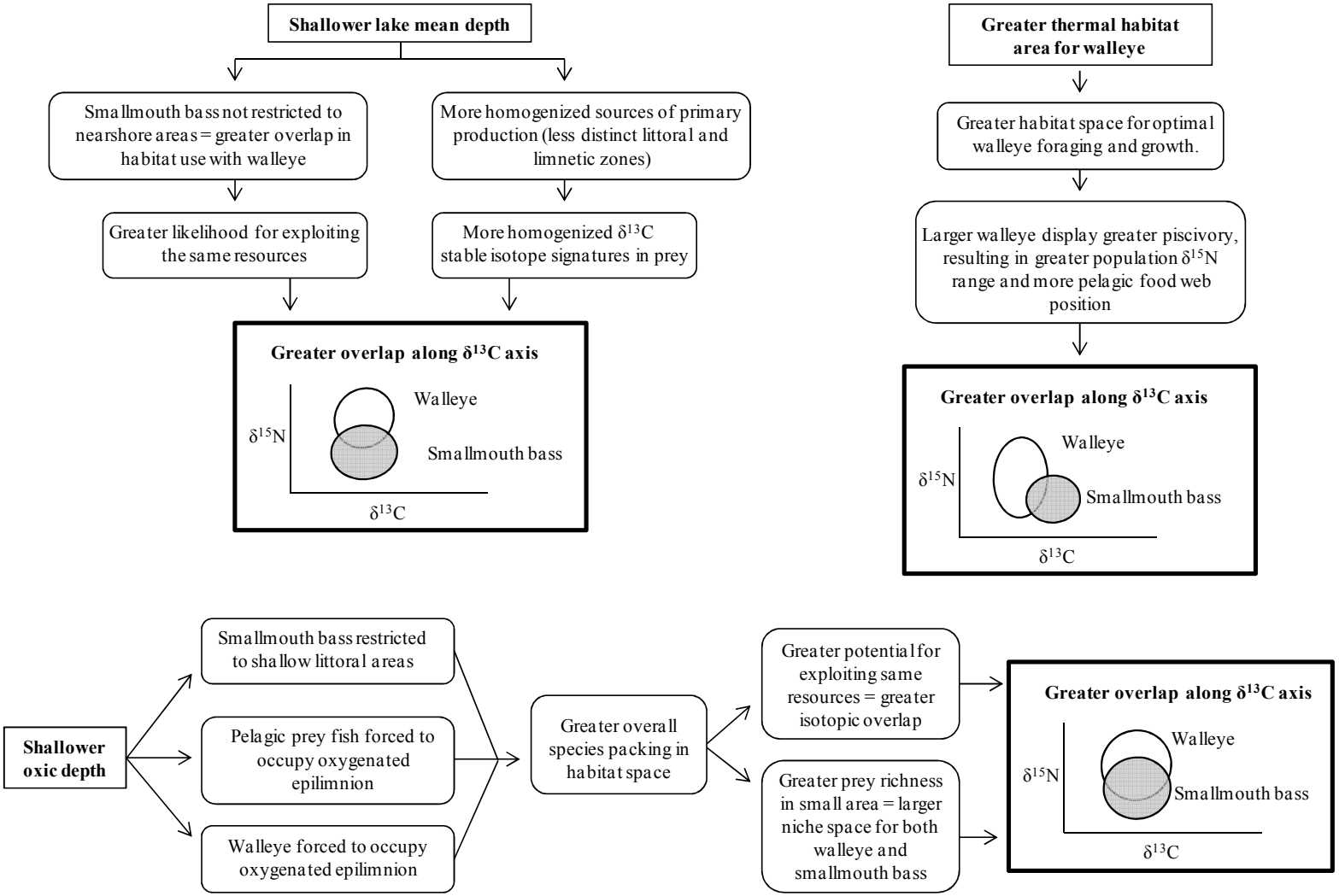

Figure 2. Conceptual diagram of hypothesized responses of walleye and smallmouth bass feeding behaviour, isotopic niche dimensions, and isotopic niche overlap to changes in primary habitat variables, if all other variables were held constant.

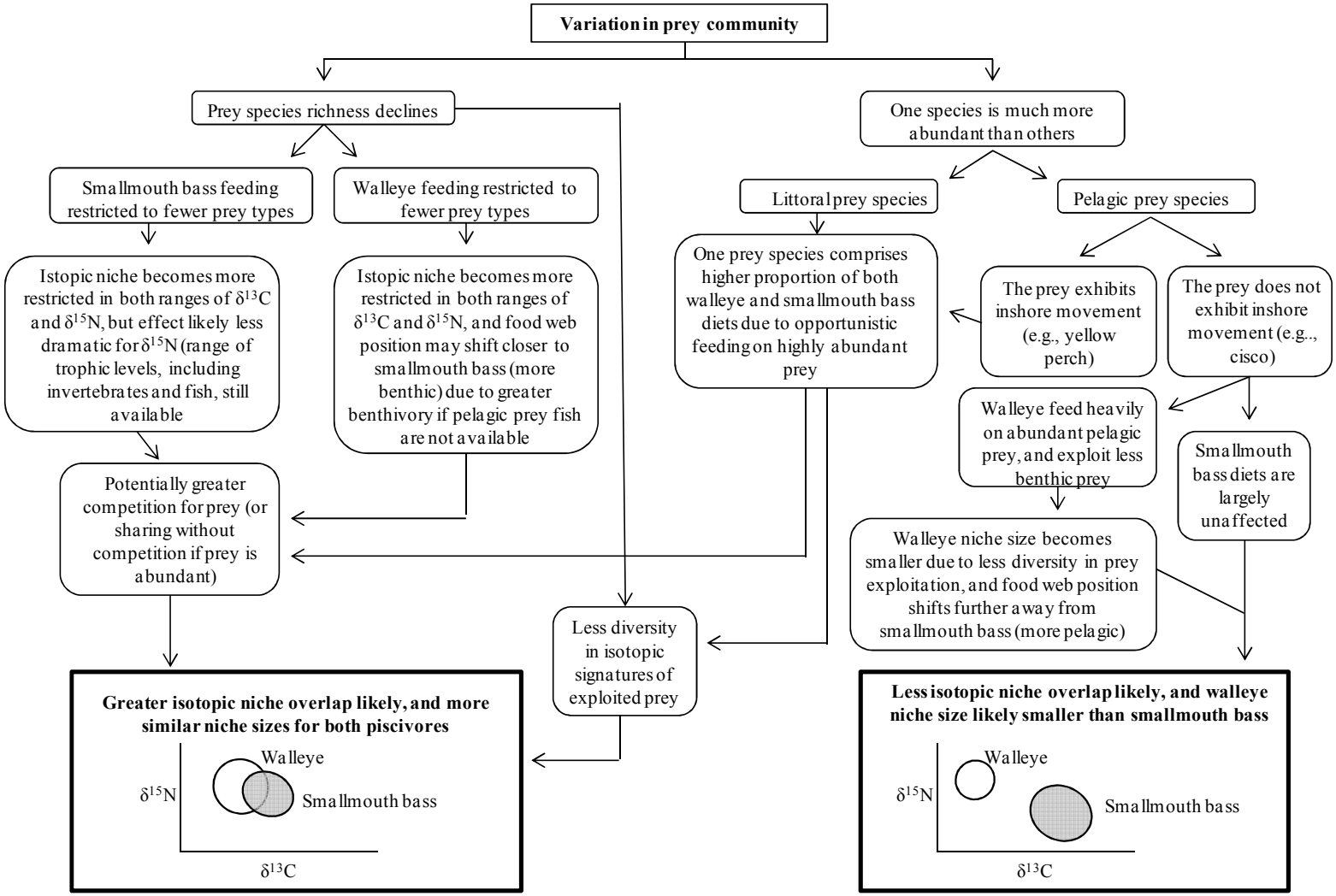

Figure 3. Conceptual diagram of hypothesized responses of walleye and smallmouth bass feeding behaviour, isotopic niche dimensions, and isotopic niche overlap to changes in prey species community, if all other variables were held constant.

species I also included four study lakes (two clear and two dark) that contained walleye without smallmouth bass, and two study lakes (one clear and one dark) that contained smallmouth bass without walleye. Sampling took place from August to October 2010 and from June to September 2011.

Ten to 20 individuals of each species were collected from each lake across a wide size gradient using a combination of gill nets, trap nets, and angling. Fork length (FL), total length (TL), weight, sex, maturity, and stomach contents were recorded for each fish, and a dorsal, skinless muscle sample was taken for stable isotope analysis. Fish of FL < 100 mm were considered unlikely to be piscivorous (Mittelbach and Persson 1998) and were not sampled. Snails (n = 10 to 60) and unionid mussels (n = 4 to 10) were also collected from each lake when available to provide benthic and pelagic isotopic baseline, respectively, for inter-lake comparisons (Post 2002). Secchi depth, dissolved oxygen profiles, and temperature profiles were determined, and subsurface water samples were collected from the estimated deepest point of each lake at the time of fish collection. Water samples were kept on ice and analyzed for alkalinity, conductivity, pH, major nutrients (DIC, DOC, total N, $NH_3 + NH_4^+$, $NO_3^- + NO_2^-$, total P, SO_4^{2-}), metals (Al, As, B, Ba, Cu, Fe, Mg, Mn, Ni, Si, Sr , Ti, Zn), and other major ions (Ca^{2+}, Cl^-, K^+, Na^+,) and within 5 days of collection by the Ontario Ministry of the Environment Chemistry Laboratory in Dorset, ON.

I chose three indices of water clarity, each of which has a slightly different effect on fish vision: Secchi depth, true colour, and DOC concentration. Secchi depth was considered the primary index of water clarity because it is strongly influenced by light scatter from suspended particles in the water column (Scheffer 2004). The ability of a fish

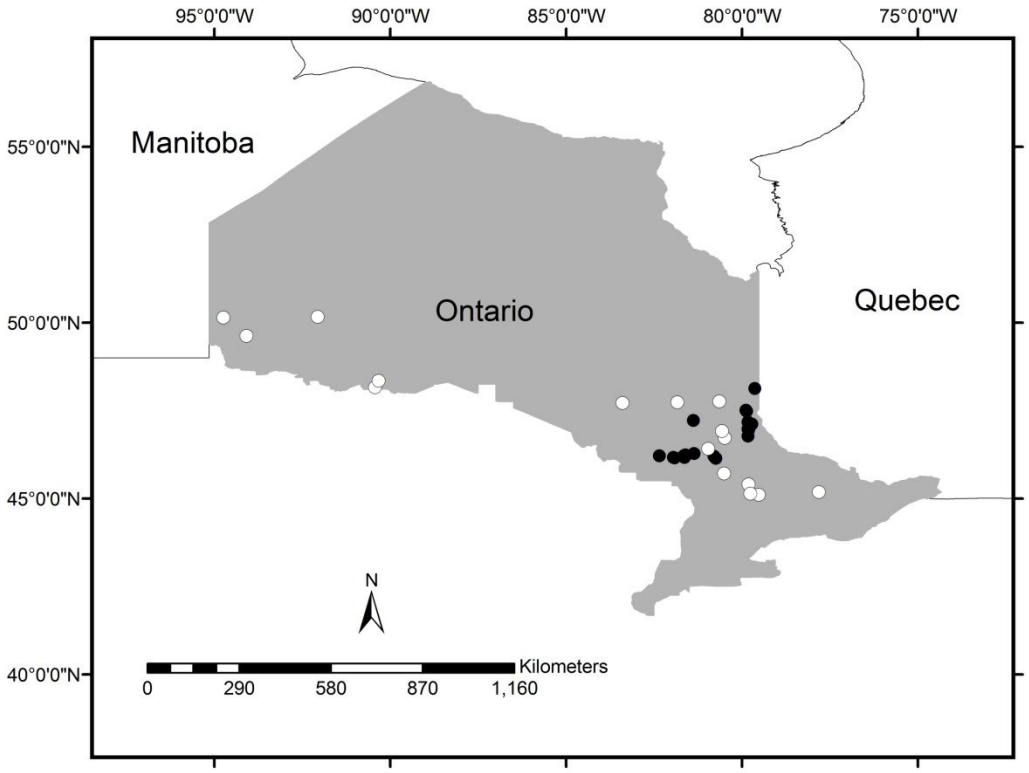

Figure 4. Distribution of study lakes. Open circles indicate lakes with available quantitative fish community data, and black circles indicate lakes with no available fish community data.

Table 1. Summary of location, growing degree days (GDD) > 5° C, area, water clarity indices, depth, morpho-edaphic index (MEI), and presence of walleye (W) or smallmouth bass (S) for study lakes.

Lake Name	Latitude	Longitude	GDD > 5°	Surface area (ha)	Secchi depth (m)	DOC (mg/L)	True colour (TCU)	Mean depth (m)	Max. depth (m)	MEI	Species sampled
Addie*	48.17	-90.43	1453.7	114.1	2.1	8.1	27.4	2.1	3.7	23.1	W + S
Andy*	49.63	-94.09	1711.2	163.1	4.5	9.5	15	6	14.6	8.3	W + S
Augusta	46.24	-81.60	1714.8	112.8	3.7	6.6	29.2	9.3	15.3	NA	W
Bear	48.13	-79.63	1584.1	116.7	2.7	7.4	43	4.1	9.1	10.9	W + S
Blueberry*	50.15	-94.74	1688.9	104.0	1.0	11.8	52.4	2.5	4.9	11.5	W
Brandy*	45.11	-79.53	1770.5	104.8	1.2	13.1	120	3.5	7.5	9.8	W
Carafel*	46.73	-80.49	1716.9	114.6	5.5	3.2	12.6	4.1	15.3	9.6	W + S
Crooked	46.15	-80.74	1735.2	113.4	4.2	6.6	37.2	4.5	21	11.5	W + S
Cutler	46.17	-81.95	1684.8	116.7	4.5	6.1	24.6	5.9	11.4	NA	W + S
Deerhound	46.17	-81.63	1711.2	108.5	5.5	6.6	19.6	4.9	12.5	8.1	W + S
Giroux*	45.71	-80.51	1774.3	115.5	1.8	9.1	68	2.9	6.1	9.8	W + S
Herridge	46.98	-79.83	1701.5	177.5	4.4	6.8	24.2	8.6	38.1	4.2	W + S
Isabella*	45.41	-79.81	1823.0	190.5	2.6	6.6	41.2	5.4	15.4	3.7	W + S
Jacob*	48.35	-90.33	1444.9	168.7	3.5	9.6	27	3.5	11	10.7	W + S
Kakakiwaganda	46.20	-80.79	1733.3	187.9	2.8	7.3	27.8	9.6	22.9	5.4	W + S
Little Panache	46.28	-81.36	1725.3	130.6	5.7	5.4	8.6	9.7	26.2	7.3	W + S
Makami*	47.74	-81.84	1534.7	169.6	3.7	8.7	41	2.3	14	18.1	W + S
Maple	46.16	-81.92	1687.3	144.4	4.0	5	16.2	7.8	14.3	4.4	W + S
McFarlane*	46.42	-80.96	1730.3	140.6	4.9	4.5	12.6	7.3	20.1	15.2	W + S
McLennan*	47.72	-83.40	1429.0	72.8	5.5	7.6	10.6	7.9	31	5.9	W
Opeechee	46.78	-79.83	1718.3	180.9	3.6	6.5	22.4	3.3	9.8	19.6	W + S
Pike	47.49	-79.86	1618.4	196.1	3.0	6.4	57	1.2	3	44.8	W + S

Lake Name	Latitude	Longitude	GDD > 5°	Surface area (ha)	Secchi depth (m)	DOC (mg/L)	True colour (TCU)	Mean depth (m)	Max. depth (m)	MEI	Species sampled
Pishabo	47.12	-79.72	1684.1	138.4	4.3	3.9	12.4	7.8	19.8	8.8	W + S
Rawson*	46.92	-80.57	1706.6	158.6	5.7	3.5	4.8	5.6	26	5.2	S
Richardson*	50.17	-92.06	1612.7	190.4	5.8	6.4	10	12.1	22.9	3.9	W + S
Salmon Trout*	45.19	-77.81	1782.9	99.6	4.1	5.4	21	6.1	13	8.2	W + S
Shillington*	47.77	-80.65	1589.4	136.0	5.5	6.4	10	11.2	34.7	5.5	W + S
Shoofly	47.23	-81.38	1660.8	185.2	8.6	3.6	5.4	11.1	48.8	16.8	W + S
Smith	46.22	-82.34	1710.8	150.0	2.7	8.3	35	NA	NA	NA	W + S
St. Leonard	46.22	-81.64	1712.1	151.8	4.5	4.4	36.6	12.8	27.5	2.3	W + S
Stewart*	45.14	-79.76	1860.8	150.1	3.8	7.6	39.6	6.6	20.4	8.7	S
Thieving Bear	47.18	-79.83	1674.2	114.8	3.9	5.1	17.2	7.4	29	5.4	W + S
Twin	47.52	-79.88	1614.5	190.4	4.6	3.9	49.8	6.2	24	9	W + S
Wilson	46.96	-79.81	1706.9	115.7	5.4	5.6	15.8	5.1	22	7.9	W + S

* Fish community composition and relative abundance data available

to detect an object such as a prey item is largely based on the contrast between the object and the background (Pitcher 1993). Under water, high scatter of image-delivering photons from suspended particles between the object and the fish's eye results in lower contrast (Douglas and Djamgoz 1990), and consequently causes shorter reaction distances from both predators and prey. True colour of the water (suspended particles removed) and DOC concentration have a greater influence on light absorption (Scheffer 2004), and thus on light availability in the water column.

Fish dorsal muscle, snail whole viscera (shell removed, pooled by size for small individuals), and unionid mussel foot muscle were analyzed for stable isotopes of nitrogen and carbon. All tissues were freeze-dried (Labconco Freezone 12 freeze drier), ball-milled (Retsch MM 301) to a fine powder and stored in glass scintillation vials. Tissue samples were then analyzed using a Finnigan Mat delta Plus continuous-flow isotope-ratio mass spectrometer connected to a Thermoquest NC2500 elemental analyzer (EA-CFIRMS) at the Stable Isotopes in Nature Laboratory (University of New Brunswick, NB). Stable isotope ratios were expressed as parts per thousand (‰) delta values of heavy isotope relative to international standards (atmospheric nitrogen for nitrogen and PeeDee Belemnite for carbon) using the formula:

$$\delta^{15}\mathrm{N} \text{ or } \delta^{13}\mathrm{C} = \left[\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 1000$$

where R represents the ratios of heavy to light isotopes ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). Lipid correction was not considered necessary as lipid content was low (Post et al. 2007) in both species of fish (mean C:N ratio was 3.23 and 3.31 for walleye and smallmouth bass, respectively) and invertebrates (mean C:N ratio was 4.48 and 4.16 for snails and clams, respectively). Robust regressions with MM-estimation (Rousseeuw et al. 2012) of TL vs.

weight, and of weight vs. $\delta^{15}N$ were used to detect outliers (1.6% of sampled individuals removed). Fish $\delta^{15}N$ values were standardized to a 1 kg mass fish for each population to account for covariation between body size and trophic level (Romanuk et al. 2011).

Relative abundance data for fish communities from 16 study lakes were obtained from the Ontario Ministry of Natural Resources' (OMNR) Broad-scale Monitoring (BsM) Program which uses a depth-stratified, quantitative gill-netting protocol (Sandstrom et al. 2011). Catch-per-unit-effort (CPUE) was calculated from the BsM data as relative biomass (total weight of fish per overnight set of a standard gill net) for four species: walleye, smallmouth bass, one littoral prey fish (yellow perch), and one pelagic prey fish (cisco). Other species were not present in enough study lakes to apply robust statistical tests. Only individual yellow perch and cisco < 50 g were used to calculate CPUE to restrict estimates to prey-sized individuals. Missing weights were estimated from total lengths using previously developed standard regression equations (walleye, Murphy et al. 1990; yellow perch, Willis et al. 1991; smallmouth bass, Kolander et al. 1993; cisco, Fisher and Fielder 1998) and verified with length-weight scatterplots. Prey species richness was calculated as the total number of potential forage species detected by the BsM survey (i.e., the top predator species walleye, smallmouth bass, largemouth bass, lake trout, northern pike, and muskellunge, and the large-bodied benthivores white sucker and lake whitefish were excluded).

Calculation of Isotopic Niche Dimensions and Niche Overlap

Five quantitative metrics of niche "dimension" were calculated for each population based on stable isotope data plotted in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space (Table 2). The first two metrics were taken from Layman et al. (2007). The first metric, mean

distance to centroid (CD), was used as an index of a population's trophic diversity and was calculated as the mean Euclidean distance of each individual to the population centroid. The second metric, standard deviation of nearest-neighbour distance (SDNND), was used as an index of trophic evenness and was calculated as the standard deviation of Euclidean distances of each individual to its nearest neighbour. The third metric, based on the work of Jackson et al. (2011), was the area of a standard ellipse (SEA) drawn around sampled individuals, which was used as an index of total niche space occupied by the population. The standard ellipse is a bivariate equivalent to standard deviation in univariate data where the size, shape, and rotation are defined by the covariance matrix associated with x and y, and the location is defined by the means of x and y (centroid at point $\bar{x}, \bar{y}$; see Batschelet 1981). SEA is then given by πab, where a is the length of the major axis and b is the length of the minor axis, both defined by the covariance matrix (see Appendix B and Batschelet 1981 for further detail). Using variation ellipses rather than traditional polygons (e.g., Layman et al. 2007) circumvents bias created by the disproportionate influence of outliers and uneven sample sizes (Jackson et al. 2012). The ellipse, however, best describes data that fit a bivariate normal distribution. Where data are not bivariate normal and create abstract shapes in biplot space, polygons may be more appropriate for delineating the population's isotopic trophic niche space. The assumption of multivariate normality was checked with visual assessment of data distributions within ellipses and with multivariate Shapiro-Wilk tests. The relative influence of individuals with atypical isotopic composition on the size of the trophic niche estimated from a polygon, however, should be carefully scrutinized. Here, I expanded the standard ellipse to capture 2 SD of data. Expanded ellipse areas (SEA_E) captured approximately 90% of

Table 2. Summary of quantitative metrics of isotopic niche dimensions for a species calculated from stable isotope data of individuals plotted in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space.

Symbol	Metric	Ecological interpretation
CD	Mean distance to centroid	Index of trophic diversity, where lower values indicate lower trophic diversity (Layman et al. 2007)
SDNND	Standard deviation of nearest-neighbour distances	Index of trophic evenness, where lower values indicate greater trophic evenness (Layman et al. 2007)
SEA_E	Standard ellipse area, expanded to capture 2 SD	Index of total isotopic niche space occupied by a population (adapted from Jackson et al. 2011)
CR_E	Carbon range of expanded ellipse	Estimate of the breadth of dietary carbon sources exploited by a population (adapted from Layman et al. 2007)
NR_E	Nitrogen range of expanded ellipse	Estimate of the range of trophic levels occupied by a population (adapted from Layman et al. 2007)

data points for this dataset (95% confidence interval of observations approaches 2 SD as *n* approaches infinity). A correction for small sample size (Jackson et al. 2011) was also applied to all SEA_E calculations. The fourth and fifth metrics of isotopic niche dimension, carbon range (CR_E) and nitrogen range (NR_E), were adapted from Layman et al. (2007) as the ranges covered by the expanded standard ellipse along the $\delta^{13}C$ and $\delta^{15}N$ axes, respectively. CR_E is an indication of the breadth of dietary carbon sources exploited by the population, while NR_E is an indication the range of trophic levels occupied by the population. By using the "shadow" cast on the axes by the ellipse, rather than the difference between individuals with the highest and lowest values on each axis, disproportionate inflation of CR_E and NR_E by atypical individuals is avoided.

Metrics of isotopic niche dimensions were then used to calculate seven isotopic interaction metrics between sympatric populations (Table 3). Isotopic niche overlap within a lake was measured as the proportion of total ellipse space occupied in overlap using the equation:

$$1.\ \%\ \text{Isotopic Overlap} = \left[\frac{(\text{area of overlap between } SEA_{E1} \text{ and } SEA_{E2}) \times 2)}{SEA_{E1} + SEA_{E2}} \right] \times 100$$

where SEA_{E1} and SEA_{E2} are the ellipse areas calculated from the walleye and smallmouth bass samples, respectively (Figure 5). In other words, the sum of SEA_E for both species was considered the total space available for isotopic niche interaction, and the overlap between the two ellipses was considered the proportion of potential space actually involved in the isotopic interaction (keeping in mind that the overlap "area" exists on both niches and thus must be multiplied by 2). Other isotopic interaction metrics calculated

Table 3. Summary of quantitative metrics of isotopic interaction between two sympatric species calculated from stable isotope data of individuals plotted in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space. All difference variables were calculated as smallmouth bass niche metrics subtracted from walleye niche metrics.

Symbol	Metric	Ecological Interpretation
Isotopic overlap	Percent overlap between expanded standard ellipses of two species	Percent of overlap between species isotopic niches
DBC	Euclidean distance between species centroids	Index of how much two species differ in their mean food web position
N Overlap	Overlap of species ellipses along the $\delta^{15}N$ axis	Index of similarity between species trophic levels
C Overlap	Overlap of species ellipses along the $\delta^{13}C$ axis	Index of similarity between species diet sources
SEA_{DIFF}	Difference between species ellipse areas	Index of how large one species niche is relative to another
CD_{DIFF}	Difference between species mean distance to centroid	Index of relative trophic diversity
$SDNND_{DIFF}$	Difference between species SD of nearest-neighbour distances	Index of relative trophic evenness

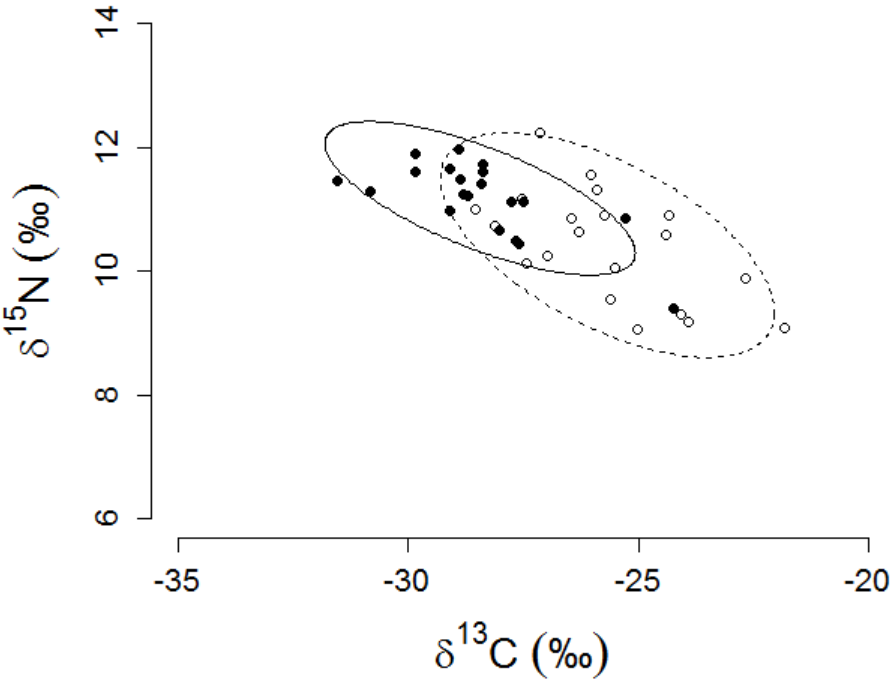

Figure 5. Example of expanded standard ellipses based on 2 SD of bivariate data, drawn for sympatric walleye (black circles, solid ellipse) and smallmouth bass (open circles, dashed ellipse) sampled from Twin Lake, Ontario. Each point is an individual fish.

for sympatric populations (where walleye = species 1, and smallmouth bass = species 2) were:

2. DBC: Euclidean distance between population centroids.
3. N Overlap: overlap of ellipse $\delta^{15}N$ ranges between two species, calculated as $(overlap_{\delta 15N} \times 2) / (NR_1 + NR_2)$. This is an index of similarity between species trophic levels, where 0 indicates completely different trophic levels and 1 indicates identical trophic levels.
4. C Overlap: overlap of ellipse $\delta^{13}C$ ranges between two species, calculated as $(overlap_{\delta 13C} \times 2) / (CR_1 + CR_2)$. This is an estimate of similarity between species dietary carbon sources, where 0 indicates completely different diet sources and 1 indicates potentially identical dietary carbon sources (albeit, one must be careful to acknowledge the inherent assumptions in using $\delta^{13}C$ as an indicator of diet source, see Cole et al. 2011)
5. SEA_{DIFF}: difference in expanded standard ellipse areas between two species, calculated as $SEA_{E1} - SEA_{E2}$. This is an indication of how large the niche of species 1 is relative to species 2, where negative numbers indicate that species 2 has a larger niche. Absolute values of SEA_{DIFF} indicate similarity in species niche ellipses regardless of which is larger, where 0 indicates identical niche size.
6. CD_{DIFF}: difference in mean distances to centroid between two species, calculated as $CD_1 - CD_2$. This is an indication of the extent of trophic diversity of species 1 relative to species 2, where negative numbers indicate that species 2 has greater trophic diversity than species 1. Small absolute values of CD_{DIFF} indicate similarity in trophic diversity regardless of which species is greater.

7. $SDNND_{DIFF}$: difference in standard deviation of nearest neighbour distance between the two species within a lake, calculated as $SDNND_1 - SDNND_2$. This is an indication of relative trophic evenness, where negative numbers indicate that species 2 has greater trophic evenness than species 1.

Measurements of isotopic interaction have the advantage that they are relative rather than absolute, rendering isotopic baseline correction unnecessary (no significant difference between corrected and uncorrected % isotopic overlap (metric 1); *t*-test, $t = -0.17$, $n = 22$, $p = 0.87$).

Analysis of Individual Species Niche Metrics

Niche dimension responses to environmental variables were first examined for each species separately (n = 62 populations). Baseline correction was necessary for analyses comparing absolute values across lakes for a single species. Fish $\delta^{15}N$ values were corrected by: $\delta^{15}N_{fish}$ – mean $\delta^{15}N_{mussel}$. Mussel was used as the $\delta^{15}N$ baseline instead of snails due to lower and more consistent within-lake variation. It has been argued that using a two-source equation to estimate trophic position is most appropriate when the goal is to compare absolute trophic positions (Vander Zanden et al. 1999; Post 2002). Such models use both snail and mussel $\delta^{13}C$ to estimate the proportion of consumer nitrogen that is derived from benthic and pelagic habitats, respectively, and adjust consumer $\delta^{15}N$ using snail and mussel $\delta^{15}N$ according to their estimated proportions in the diet. Estimates based on two-source models, however, are often similar to estimates based on a single baseline organism and are most effective when baseline $\delta^{13}C$ has a strong linear relationship with baseline $\delta^{15}N$ (Post 2002), which was rare in my

study lakes. Following Post (2002), fish $\delta^{13}C$ was transformed into a proportion of the dietary carbon that is derived from the pelagic food web by using lake-specific pelagic (mean of unionid mussel) and benthic (mean of snail) $\delta^{13}C$ endpoints: $(\delta^{13}C_{fish} - \delta^{13}C_{snail}) / (\delta^{13}C_{mussel} - \delta^{13}C_{snail})$. Lakes without sufficient baseline data (n = 12) were excluded from individual species analyses.

Each baseline-corrected isotopic niche dimension metric was then linearly regressed against each habitat and community variable (Secchi depth, DOC, true colour, thermal optical habitat area for walleye (TOHA; Lester et al. 2004), depth of oxic zone, depth of anoxic zone, mean depth, morpho-edaphic index (MEI, an indication of lake productivity; Ryder 1965), yellow perch CPUE (< 50 g), walleye CPUE, smallmouth bass CPUE, and prey species richness) separately for each species. Cisco CPUE data was not available from enough baseline-corrected lakes to make it a valid variable in these models. Although species responses to environmental gradients are often unimodal rather than linear (Soinen et al. 2011), prior visual assessment of scatterplots indicated that no clear non-linear relationships existed between niche dimension metrics and environmental variables (Appendix C).

Isotopic Overlap Analysis

Mean $\delta^{15}N$ and $\delta^{13}C$ of sympatric walleye and smallmouth bass were compared across all dual-species lakes with paired-comparisons t-tests to test for differences in general niche location. Metrics of isotopic niche dimensions (Table 2) were also compared between species across all lakes with paired-comparisons t-tests. Isotopic interaction metrics (Table 3) were then calculated for each pair of sympatric populations and linear regressions of all isotopic interaction metrics were performed against water

clarity indices (Secchi depth, DOC, and true colour). All data were examined for outliers and for violations of homoscedasticity and normality. Where it improved normality, proportional data (i.e., overlap metrics) were arcsine-square-root-transformed and linear data were $\log_{10}(x+1)$-transformed.

To explore other potential predictors of isotopic overlap besides water clarity, stepwise multiple regressions of each isotopic interaction metric were performed against standardized habitat variables. Water chemistry variables (including true colour and DOC) were reduced using principal components analysis (PCA). Variables were $\log_{10}(x+1)$ or square-root-transformed where necessary to improve normality prior to analysis. Habitat variables were removed where they caused collinearity (variation inflation factor > 10). Stepwise multiple regressions for all lakes were run with Secchi depth, TOHA, depth of oxic zone, depth of anoxic zone, lake mean depth, MEI and the first 4 principal components (cumulatively explaining 69% of variation in water chemistry). Mean depth and MEI were of special interest since they have previously been identified as important factors determining the presence of walleye and smallmouth bass in north-temperate lakes (Johnson et al. 1977). Since mean depth and MEI were correlated, multiple regressions were repeated once with mean depth included as a predictor, and once with MEI included as a predictor. Stepwise multiple regressions for dual-species lakes with available community data (n = 11) were run with Secchi depth, TOHA, depth of oxic zone, prey species richness, and CPUE of cisco, yellow perch, walleye, and smallmouth bass. Criteria (Prob > partial-F) for variable entry and retention in the model were set at 0.5 and 0.05, respectively.

Studies of smallmouth bass effects on lake trout have found that lake trout are more resilient against bass invasion when pelagic prey fish are present in the lake (Vander

Zanden et al. 1999). To identify if this trend was true for walleye as well, I examined whether the absence of pelagic prey fish led to greater niche overlap between walleye and smallmouth bass. Only two of my study lakes with available community data had no pelagic prey fish (identified as yellow perch, cisco, and rainbow smelt for these systems), so I was restricted to visual assessment of ellipses and comparison of isotopic overlap metrics of lakes without pelagic prey to mean values of lakes with pelagic prey.

Multiple regressions were performed in SAS ver. 9.2. PCAs of water chemistry data were performed in SPSS ver. 19. All other statistical procedures were performed in R (ver. 2.14, R Development Core Team 2011) using the packages robustbase (Rousseeuw et al. 2012), ellipse (Murdoch and Chow 2012), mvnormtest (Jarek 2012), car (Fox and Weisberg 2011), gvlma (Pena and Slate 2010), spatstat (Baddeley and Turner 2005), and siar (Parnell and Jackson 2011). R code modified from the siar package for ellipse expansion, and the calculation of NR_E, CR_E, and percent overlap is provided in Appendix B. A null hypothesis was rejected at the $\alpha = 0.05$ significance level for all statistical tests.

RESULTS

Analysis of Individual Species Niche Metrics

Water clarity had a significant effect on niche dimensions for individual species. Total occupied niche space (SEA_E) significantly increased with true colour for smallmouth bass ($F_{1,19} = 5.02$, $p = 0.04$, $r^2 = 0.21$), but not for walleye ($F_{1,19} = 0.4$, $p = 0.53$, $r^2 = 0.02$; Figure 6a). No significant relationships existed for either species between SEA_E and DOC (walleye: $F_{1,19} = 0.66$, $p = 0.86$, $r^2 < 0.01$; smallmouth bass: $F_{1,19} = 0.114$, $p = 0.74$, $r^2 = 0.01$) or Secchi depth (walleye: $F_{1,17} = 2.3$, $p = 0.15$, $r^2 = 0.12$;

smallmouth bass: $F_{1,17} = 1.42$, $p = 0.25$, $r^2 = 0.08$). Smallmouth bass exploited a wider range of dietary carbon sources, but occupied an increasingly restricted range of trophic levels with increasing water clarity, as indicated by significant positive relationships between CR_E and Secchi depth ($F_{1,19} = 5.94$, $p = 0.03$, $r^2 = 0.26$; Figure 6b), and between NR_E and true colour ($F_{1,19}=7.43$, $p = 0.01$, $r^2 = 0.28$; Figure 6c), respectively. Walleye also exhibited greater trophic evenness (lower values of SDNND) with increasing water clarity, as indicated by a significant positive relationship between SDNND and true colour ($F_{1,19} = 4.55$, $p = 0.05$, $r^2 = 0.19$; Figure 6d). All water clarity indices were significantly linearly correlated with each other (Secchi depth and DOC: $F_{1, 32} = 30.48$, $p < 0.01$, $r^2 = 0.49$; Secchi depth and true colour: $F_{1, 32} = 36.01$, $p < 0.01$, $r^2 = 0.54$; DOC and true colour: $F_{1, 32} = 23.89$, $p < 0.01$, $r^2 = 0.43$).

Isotopic Overlap Analysis

Despite trophic responses of smallmouth bass to water clarity, there was little evidence that water clarity had a substantial impact on trophic interactions with walleye. Isotopic overlap between walleye and smallmouth bass ranged from 0 to 65%, but there were no significant correlations between water clarity indices and trophic interactions of walleye and smallmouth bass in my study lakes. No measurement of isotopic overlap (percent isotopic overlap, N overlap, or C overlap) was found to be significantly linearly related to any of the water clarity indices. The size of walleye and smallmouth bass isotopic niches became more similar with increasing DOC, as evidenced by a significant negative correlation between SEA_{DIFF} and DOC ($F_{1,26} = 7.75$, $p = 0.01$, $r^2 = 0.23$; Figure 7a). Walleye also appeared to have lower trophic evenness relative to smallmouth bass ($SDNND_{DIFF}$) as waters became darker, as indicated by a marginally insignificant

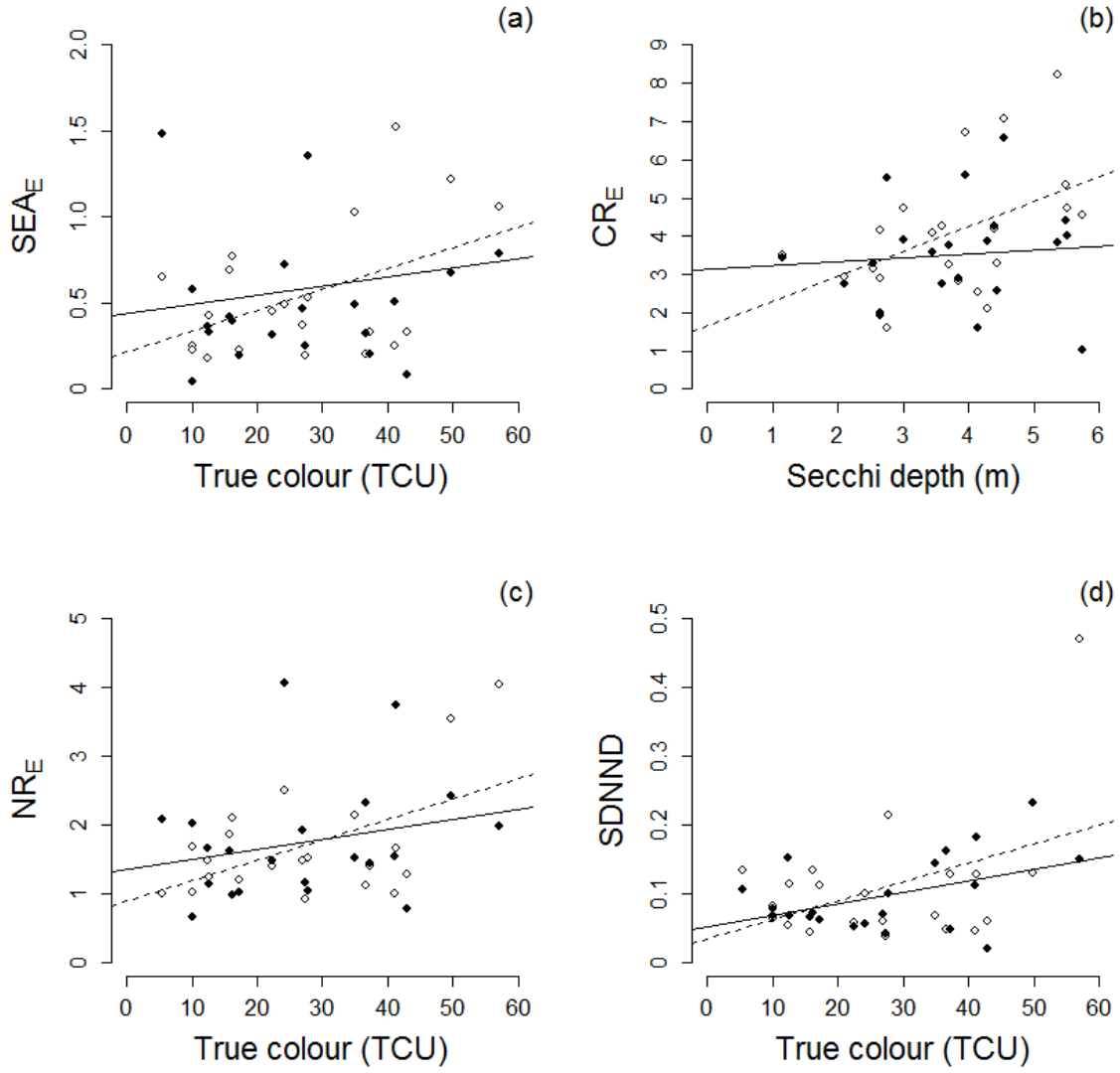

Figure 6. Linear regressions of walleye (black circles, solid line) and smallmouth bass (open circles, dashed line) niche dimension metrics that had significant relationships with water clarity indices: (a) isotopic niche size (SEA_E) against true colour, (b) breadth of dietary carbon sources exploited by the population (CR_E) against Secchi depth (m), (c) range of trophic levels occupied by the population (NR_E) against true colour (TCU), and (d) trophic evenness (SDNND) against true colour. Only smallmouth bass SEA_E, CR_E, and NR_E had significant relationships with water clarity, while only walleye SDNND had a significant relationship with water clarity.

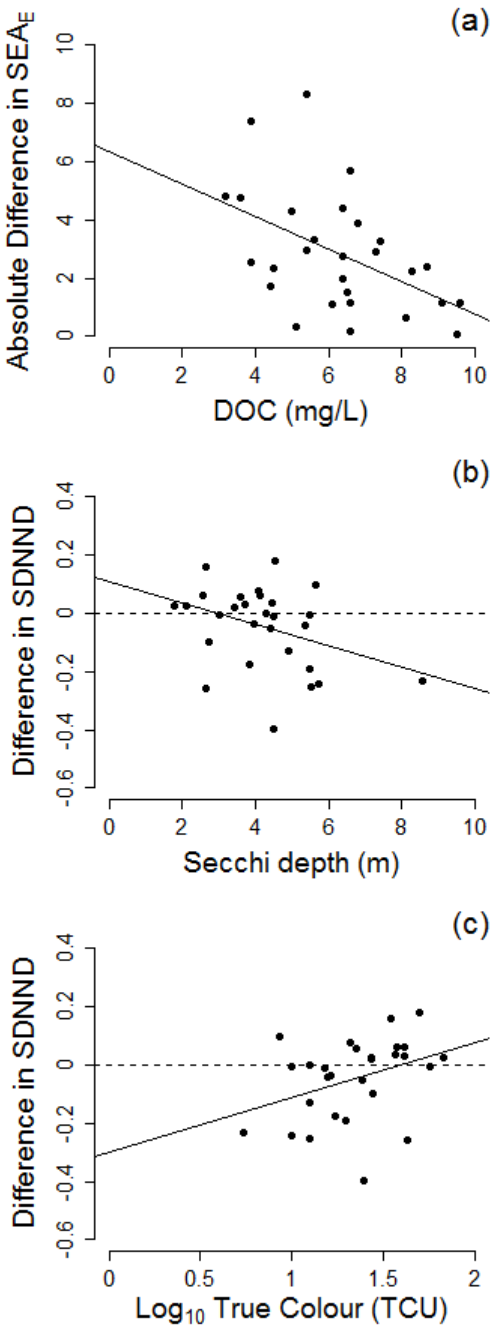

Figure 7. Linear regressions of walleye-smallmouth bass isotopic interaction metrics that had significant relationships with water clarity indices: (a) absolute difference in SEA_E against DOC (mg/L), (b) the difference in standard deviation of nearest neighbour distances (SDNND) against Secchi depth (m) and (c) the difference in standard deviation of nearest neighbour distances (SDNND) against $\log_{10}$-transformed true colour (TCU). Dotted lines indicate no difference in SDNND between species. Walleye have greater SDNND above zero, and smallmouth bass have greater SDNND below zero.

negative correlation with Secchi depth ($F_{1,26} = 4.03$, $p = 0.06$, $r^2 = 0.13$; Figure 7b), and a marginally insignificant positive correlation with $\log_{10}$-transformed true colour ($F_{1,26} = 4.03$, $p = 0.06$, $r^2 = 0.13$; Figure 7c).

There were significant differences between walleye and smallmouth bass mean $\delta^{15}N$ (paired-comparisons t-test; t = 14.14, n = 28, $p < 0.001$) and $\delta^{13}C$ (paired-comparisons t-test; t = -5.13, n = 28, $p < 0.001$), indicating that walleye generally fed at a higher trophic level and on more pelagic carbon sources than smallmouth bass. There were no significant differences between these species for any other metric of isotopic niche dimension.

Stepwise multiple regressions of all study lakes without fish community data revealed that walleye and smallmouth bass fed on more isotopically similar carbon sources as lake mean depth became shallower, as evidenced by a significant negative relationship between C Overlap and mean depth ($F_{1,25} = 6.54$, $p = 0.017$, $r^2 = 0.21$). Walleye niche size (SEA_E) was also larger relative to smallmouth bass in lakes with a shallow oxic depth ($F_{1,25} = 6.62$, $p = 0.02$, $r^2 = 0.22$). Similarly, trophic diversity was more similar between species as oxic depth became shallower, as indicated by a significant positive relationship between absolute CD_{DIFF} and the depth of the oxic depth zone ($F_{1,25} = 5.32$, $p = 0.03$, $r^2 = 0.19$).

Stepwise multiple regressions of lakes with fish community composition data revealed that the size of walleye and smallmouth bass niches became more similar as the number of available prey types decreased ($F_{1,9} = 12.42$, $p = 0.01$, $r^2 = 0.61$), as indicated by a significant positive relationship between absolute SEA_{DIFF} and prey species richness. Neither species niche size was consistently larger in lakes with high prey species richness. Walleye and smallmouth bass niches also occupied a more similar food web position in

lakes with high yellow perch abundance, as indicated by a significant negative relationship between DBC and yellow perch relative abundance ($F_{1,9} = 7.1$, $p = 0.03$, $r^2 = 0.47$).

There was no evidence that the lack of pelagic prey fish in two of the study lakes with fish community composition data led to greater niche overlap between walleye and smallmouth bass. Walleye and smallmouth bass niches did not overlap at all in one of these lakes (walleye were higher in trophic level and had more pelagic diets than smallmouth bass), and in the other lake the species were completely separated along the $\delta^{15}N$ axis, indicating that even if both species were exploiting resources from a similar habitat, walleye were consistently feeding at a higher trophic level.

Visual assessment of isotopic niches in lakes where one species existed without the other revealed no detectable difference from the niches of those populations in lakes where both species existed in sympatry.

DISCUSSION

Surprisingly, water clarity did not appear to play a key role in structuring trophic interactions between smallmouth bass and walleye, although water clarity did influence the trophic niche dimensions of smallmouth bass. Smallmouth bass expanded their total occupied niche space (SEA_E) in coloured waters by occupying a wider range of trophic positions (larger NR_E) while exploiting a more restricted range of dietary carbon sources (smaller CR_E). In contrast, the niche dimensions of dark-adapted walleye did not appear to be influenced by water clarity. There was no evidence that the expanded niche of smallmouth bass in darker waters increasingly overlapped with that of sympatric walleye,

suggesting that water clarity does not have a significant influence on dietary overlap. The two species did, however, feed on more isotopically similar carbon sources in shallow lakes, had more similar niche size when prey fish richness was low, and occupied more similar food web positions in lakes with high yellow perch abundance. While other studies have tested for dietary overlap between walleye and smallmouth bass and for walleye fitness responses to smallmouth bass invasions, to my knowledge this is the first study that explicitly tests for abiotic and biotic factors that could potentially influence trophic similarity and interactions of these species.

Individual Species Responses

The lack of influence of water clarity on walleye isotopic niche dimensions was surprising and contradicted my hypothesis. Although in retrospect it seems intuitive that a species adapted for dark waters may not be sensitive to water clarity changes, there is considerable evidence that adult walleye are negatively phototactic and will seek refuge from high light intensities (e.g., Scherer 1971; Scherer 1976; Ali et al. 1977; Ryder 1977; Vandenbyllaardt et al. 1991), and it is often stated that light intensity is the principal abiotic factor affecting walleye behaviour (e.g., Bulkowski and Meade 1983; Lester et al. 2004). It seems likely, however, that light does not have a large influence on prey selection despite its influence on daytime activity. Even in clear lakes walleye hunt primarily at night, so foraging takes place in low illumination regardless of whether darkness is a result of turbid waters or nightfall. The presence of pelagic forage fish could also have confounded the effect of water clarity on walleye niche dimensions if walleye restricted foraging to pelagic prey even in clear waters. However, high cisco abundance was not consistently associated with a more pelagic walleye signal despite walleye's

known preference for cisco (Ryder and Kerr 1978; Jones et al. 1994; Henderson et al. 2004).

The availability of oxygen may have also masked the effect of water clarity on walleye niche dimensions. In this study walleye occupied a larger isotopic niche (SEA_E) relative to smallmouth bass in lakes with shallow oxic depth. A larger isotopic niche generally indicates that the population (although not necessarily individuals, see Bolnick et al. 2003) was exploiting a wider range of prey items. At dissolved oxygen concentrations < 2 mg/L walleye's usual negative phototactic behaviour is overridden by their need for oxygen (Scherer 1971). In natural populations, walleye may occupy the epilimnion in hypoxic waters (Brandt et al. 2011) despite more suitable thermal and optical conditions in the metalimnion and hypolimnion (Jones et al. 2006; Brandt et al. 2011). Brandt et al. (2011) found that temporarily hypoxic waters can actually increase habitat suitability for walleye because prey fish also become concentrated in the oxygenated epilimnion, bringing preferred pelagic prey fish such as rainbow smelt (Pothoven et al. 2009) and yellow perch (Roberts et al. 2009) into closer proximity with littoral fish and invertebrate prey. Greater inter-individual variation in stable isotope signatures (i.e., larger SEA_E) could also occur if only part of the population is influenced by hypoxia. Brandt et al. (2011) confirmed that hypoxic zones can be patchy within a lake, suggesting that greater diversity in stable isotope signatures for walleye result not only from exposure to a more diverse number of prey items in the oxygenated epilimnion, but also from differential behaviour and stable isotope turnover rates of fish in oxic vs. anoxic patches (Cay and Summerfelt 1992; Rahel and Nutzman 1994; Wiedel et al. 2011). Oxygen availability also generally decreases throughout the summer in stratified lakes until it is refreshed by fall mixing. Since dissolved oxygen profiles were only taken

at the time of fish sampling, it is uncertain if the sampled populations in this study were exposed to oxygen depletion long enough to create a true response in stable isotope values or if the effect of oxygen is "noise."

Trophic responses of smallmouth bass to water clarity were consistent with my hypothesis that bass isotopic niche dimensions would contract as waters became clearer. This contraction was mainly a result of exploiting a more limited range of trophic levels (NR_E) in clearer waters, which is consistent with laboratory observations of increased selectivity for free-swimming (rather than benthic) prey fish in clear relative to turbid waters (Carter et al. 2010). Greater selection for fish over invertebrate prey makes sense in light of their energetic profitability, but only when foraging for them does not require extensive energy expenditure as it would when visibility is low. In the boreal systems studied here, the majority of small-bodied littoral fish are planktivorous. Similarity in feeding behaviours among prey fish species would result in similar trophic positions, which would in turn narrow the NR_E in piscivore populations that exploit a larger proportion of them. The increased prey selectivity for pelagic fish in aquaria (Carter et al. 2010) is also consistent with smallmouth bass exploitation of a wider $\delta^{13}C$ range (CR_E) in clearer waters in this study. Expanding CR_E with lower Secchi depth suggests the population was able to venture deeper and supplement their diets with pelagic prey as visual acuity increased, making visual foraging for fish less energetically costly. Secchi depth is most strongly influenced by light scatter, which influences the ability of a fish to distinguish an object against the background (Scheffer 2004). Object detection against a uniform open water background is likely more difficult than against the variable littoral background where the contrast of the object changes as it moves among obstacles,

making low light scatter (i.e., high Secchi depth) necessary for efficient bass foraging in the pelagic zone.

In contrast, smallmouth bass consumption of crayfish, which has also been shown to increase with turbidity (Carter et al. 2010), could contribute to greater variation in bass $\delta^{15}N$ signatures due to the high inter-individual variation in crayfish diets (Taylor and Soucek 2010). Crayfish were common in smallmouth bass stomachs in this study (data not shown), but stomach content data were not sufficient to confirm if consumption was greater in coloured waters. The isotopic niche shifts observed in this study agree with previous observations that low illumination has a negative impact on smallmouth bass feeding efficiencies (Skewa and Hartman 2003; Carter et al. 2010).

Apparent shifts in food web position and niche dimensions estimated from stable isotopes may actually be a result of shifts in the isotopic composition of available carbon rather than changes in consumer feeding behaviour. In lakes with high DOC concentrations, food webs are primarily based on energy mobilized from bacterial production that can use DOC directly as a resource (Jansson et al. 2000; Ask et al. 2009; Solomon et al. 2011). Dissolved CH_4 and CO_2 produced during bacterial respiration is depleted in ^{13}C relative to terrestrial plant detritus or phytoplankton (Woltemate et al. 1984), which could cascade into consumers at higher trophic levels and result in more negative $\delta^{13}C$ signatures. Such a change could be erroneously interpreted as a shift towards a more pelagic diet with decreasing water clarity. Increased reliance of both pelagic and benthic food webs on heterotrophic production would also lessen the difference between pelagic and benthic baseline $\delta^{13}C$ signatures and consequently restrict the maximum potential CR_E that a population could attain. Decreasing CR_E with increasing DOC was observed for smallmouth bass populations, but it was not observed

for walleye, suggesting that changes in isotopic niche dimensions were influenced more strongly by feeding behaviour than by water chemistry, which would be expected to influence all species. Moreover, changes in niche dimensions were significantly correlated to Secchi depth and true colour but not to DOC.

Isotopic Overlap and Potential for Co-Existence

Previous studies have demonstrated that walleye and smallmouth bass share prey items, with dietary overlap ranging from minimal to nearly complete (e.g., Wuellner et al. 2010; Frey et al. 2003). The results from this research also demonstrate high variation in potential for competition, ranging from 0 to 65% isotopic niche overlap. The effect of water clarity on trophic interactions, however, was minimal. Walleye and smallmouth bass niche sizes were increasingly similar in coloured waters, but this is likely linked to the availability of different prey types because niche sizes were also more similar when prey richness was low, and prey richness decreased with water clarity. The only other study to my knowledge that tests for an effect of light on competition between walleye and smallmouth bass found only a weak influence of water clarity (Wuellner 2009). However the study was conducted with starved juveniles in aquaria. Unlike adults, juvenile walleye are positively phototactic until the reflective tapetum lucidum and macroreceptors in their eyes develop around 60-70 mm (Vanderbyllaardt et al. 1991). A stronger light effect may be found if laboratory studies are conducted with adults, but the results of my study suggest that other abiotic and community factors override the influence of light on competition in wild populations.

Walleye and smallmouth bass appeared to feed on more isotopically similar carbon sources as lakes became shallower, but this is likely an artefact of the lack of

distinct littoral and limnetic zones in shallow lakes (mean depth < 4 m). Benthic algae contribute to production in both littoral and limnetic habitats, especially in shallow lakes where light can penetrate to the sediment throughout the entire water column (Ask et al. 2009; Karlsson et al. 2009). Consequently, there is greater isotopic homogeneity in basal carbon sources in shallow lakes (France 1995), weakening the ability of stable isotopes to distinguish between species diets. Additionally, the lack of distinct littoral and limnetic habitats most likely results in less habitat segregation between walleye and smallmouth bass than would otherwise occur in deeper lakes, making interspecific interactions more likely. Interestingly, this did not result in greater overall dietary overlap, likely due to exploitation of different trophic levels.

Walleye and smallmouth bass niche size was also increasingly similar with decreasing prey species richness, and they occupied more similar positions within the food web in lakes as yellow perch relative abundance increased. Fewer available prey items results in a more restricted potential niche breadth for both generalist and specialist populations (Bolnick et al. 2003). This is supported by the strong, positive relationship between the variability in niche position of freshwater fishes and species richness (Soinen et al. 2011). As species richness declines the niches of both walleye and smallmouth bass become restricted in a similar way. Competition may still be minimized, however, by temporal segregation of foraging or selection for different size-classes (Wuellner et al. 2010). Even when walleye and smallmouth bass are exploiting the same prey fish species, walleye tend to consume a larger size class than smallmouth bass (Wuellner et al. 2010) and feed primarily during crepuscular periods (Ryder 1977, Ryder and Kerr 1978) while smallmouth bass tend to hunt throughout the day (Scott and Crossman 1973).

More similar food web positions with increasing relative yellow perch abundance suggests a higher proportion of yellow perch in the diets of both predators, which have both been known to display a preference for yellow perch (e.g., Ryder and Kerr 1978; Liao et al. 2002; Frey et al. 2003). The lack of increasing niche overlap, despite having closer niche locations, may be a result of exploiting different sub-populations of yellow perch. In the presence of predators, yellow perch populations often develop distinct limnetic and littoral morphs (Lippert et al. 2007), making it possible for walleye to feed on yellow perch inhabiting limnetic areas while smallmouth bass feed on yellow perch inhabiting littoral areas. If yellow perch were partitioned in this way, the predators would have similar trophic positions but be separated along the $\delta^{13}C$ axis as was observed.

While lake depth, oxygen, and prey community explained limited proportions of variation in isotopic niche interactions, no biotic or abiotic factor tested here explained a significant amount of the variation in isotopic niche overlap. The lack of complete dietary overlap in this study may be partially due to the generalist feeding habits of both species (Scott and Crossman 1973), allowing one or both predators to switch between multiple types of prey in the presence of competitors. A food item that is preferred in the absence of a competitor is not necessarily preferred in the presence of a competitor (Engen et al. 1988). In lakes where littoral prey fish abundance is reduced by smallmouth bass, walleye could shift their diets to pelagic prey fish or benthic invertebrates.

Minimal dietary overlap despite strong competitive interactions is also possible if one species was preventing another from exploiting certain prey. Exploitative competition, whereby smallmouth bass reduced prey availability to other predators by reducing prey abundance, was identified as the likely cause of salmonid population declines in bass-invaded lakes (Vander Zanden et al. 1999; Vander Zanden et al. 2004).

Aquarium experiments demonstrated that adult smallmouth bass are also able to outcompete adult walleye for prey fish both by reacting quicker to prey (exploitative competition) and by using aggressive displays such as nipping and chasing (interference competition; Wuellner 2009). However, studies on wild populations have found little evidence for negative impacts of smallmouth bass abundance on walleye fitness, abundance, or growth (Frey et al. 2003; Nate et al. 2003; Fayram et al. 2005; Wuellner et al. 2011; Galster et al. 2012). I also found no significant relationships of walleye or smallmouth bass relative abundance with any metric of niche interaction in multiple regressions. Competition should reduce fitness in one or both predators (Birch 1957). The apparent lack of such an effect further suggests that severe competition is not a common occurrence between sympatric walleye and smallmouth bass populations on the Boreal Shield.

In a South Dakota lake where smallmouth bass were intentionally introduced, Galster et al. (2012) observed a short-term population decline from which walleye rebounded within two years. Galster et al. (2012) attributed the rebound to adapted feeding strategies since walleye stable isotope signatures switched from mainly littoral prey to mainly pelagic prey after the smallmouth bass introduction. In my study walleye usually had more pelagic diets than smallmouth bass, but clear benthic-pelagic separation between species was not consistent even in lakes where pelagic prey fish were available to walleye. Walleye tended to occupy higher trophic levels than smallmouth bass, suggesting that walleye were able to exploit energetically valuable resources despite the presence of smallmouth bass. This contrasts with stable isotope studies that revealed a clear separation between a pelagic lake trout signal and a benthic smallmouth bass signal, as well as a lower lake trout trophic position in bass-invaded lakes without pelagic prey

fish (Vander Zanden et al. 1999; Vander Zanden et al. 2004). My results suggest walleye are able to co-exist more readily than lake trout with smallmouth bass in small Boreal Shield lakes, regardless of light conditions or the absence of pelagic prey fish. Explicit comparisons of sympatric lake trout, walleye, and smallmouth bass, however, are still needed to confirm this hypothesis.

While the use of ellipses in stable isotope biplot space to define niche space is very informative, I must emphasize that overlap between species indicates *potential* for dietary overlap and competition. Without stable isotope or fatty acid data for prey, I cannot determine whether populations with isotopic overlap were exploiting the same prey resource or different prey with similar isotopic composition (Iverson et al. 2004; Layman et al. 2012). Detailed gut content analysis can assist in teasing apart diet differences between species, but the gut contents recorded for this study were too coarse to be useful. Moreover, interspecific competition is difficult to quantify in the field due to restricted observation opportunities. It has been argued that indirect methods of assessing interactions between freshwater fishes (such as stable isotopes or fitness relationships) are insufficient to directly test for competition (Almeida and Grossman 2012). The quantitative metrics of isotopic interaction calculated in this study are strong indicators of trophic responses to other species or to environmental gradients. Although these methods cannot determine the mechanism of competition, they can help identify when competition between species may be occurring in natural, unobservable populations under varying environmental conditions.

Summary and Concluding Thoughts

Together with evidence from other studies, the results of this research imply that walleye populations in smallmouth bass-invaded lakes on the Boreal Shield are not likely to experience the same grim fate as lake trout and brook trout populations. Conversations with anglers and lodge owners in northern Ontario usually did not indicate concern about the effects of bass on walleye, and many claimed that smallmouth bass had been present for as long as they could remember (pers. communication). Early examinations of percid community assemblages by Ryder and Kerr (1978) suggested that mixed percid-centrarchid assemblages could be unstable in lakes bordering between mesotrophy and eutrophy, where small changes to environmental conditions could cause one species to become dominant over the other. In northern Ontario where oligotrophic lakes are more common, Johnson et al. (1977) found that lakes with sympatric walleye and smallmouth bass were relatively uncommon but did exist well after smallmouth bass introductions had occurred in the early 1900's, suggesting that community stability had been attained. My results also suggest that walleye and smallmouth bass can co-exist in oligotrophic Boreal Shield lakes regardless of water clarity.

Co-existence between walleye and smallmouth bass, however, does not warrant bass stocking and transfers in walleye-dominated lakes. Smallmouth bass also pose a threat to walleye health via the introductions of disease and parasites (Armstrong 1985). Bass stocking in walleye lakes could also lead to unintentional transfers to lakes occupied by sensitive native predators like lake trout and brook trout, and smallmouth bass introductions can have severe consequences for the diversity of the littoral forage fish community. For instance, Jackson and Mandrak (2002) predicted that 25,000 cyprinid populations in Ontario alone will be extirpated due to smallmouth bass invasions.

In summary, I have demonstrated that trophic responses to water clarity occur for smallmouth bass, but not for walleye, and that water clarity appears to have little influence on dietary overlap between wild populations of walleye and smallmouth bass. Rather, prey fish community and lake morphometry appear to have a more significant influence on isotopic niche interactions between these two predators. This study agrees with others that found little evidence for adverse impacts of smallmouth bass on walleye fitness. The effect of water clarity on smallmouth bass trophic ecology, however, provides an additional key to understanding invasion success and may be an important variable to include in future models that predict smallmouth bass impacts on native forage fish and predators.

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APPENDIX A

A.D., Gunn, J.M., and Johnston, T.A. 2012. Role of ambient light in structuring north-temperate fish communities: Potential effects of increasing dissolved organic carbon concentration with a changing climate. Environ. Rev. 20: 173- 190.

ABSTRACT

The vertical light environment in freshwater lakes is sensitive to changes in dissolved organic carbon (DOC) concentrations, and DOC concentrations in most boreal lakes appear to be increasing as the climate changes. Understanding how DOC dynamics in lakes and watersheds are then linked to fish habitat is therefore critical to assessing the effects of climate change on fish communities. This paper reviews the evidence for climate-induced alterations to DOC in north-temperate watersheds and assesses the potential consequences of the resultant decreases in water clarity on fish production and community structure in small boreal lakes (< 500 ha). Although DOC increases are forecast for most boreal lakes, complex interactions between local climate, rates of terrestrial organic matter decomposition and runoff, existing water quality, species shifts in forest communities, and changing season lengths can all combine to affect the magnitude of water clarity declines that will occur in individual lakes. Elevated DOC concentrations will affect the availability of coldwater vs. warmwater habitat and niche characteristics that are dependent on lake depth, water clarity, and the preferences and physiological tolerances of the individual species. The shifts in availability of suitable thermal habitat will in turn affect fish growth, production, and community composition. Range expansions for warmwater species and range reductions for coldwater species will

likely occur in warmer, darker environments, with adverse consequences for some native species and likely advantages for invasive species such as smallmouth bass. Likewise, major shifts in trophic dynamics would accompany the darkening of boreal lakes as species-specific feeding efficiencies change and primary and secondary production are altered. From a beneficial perspective, elevated DOC concentrations will likely relieve some physiological stress in biota via protection against contaminant toxicity and UVR exposure. As with many other disturbances, we need to view climate change impacts on fish communities as a multiple stressor problem and the potential impacts of the changing light environment needs to be given as much prominence as the study of stressors such as eutrophication and trace contaminants.

INTRODUCTION

Water clarity conditions and associated habitat characteristics in north-temperate lakes will not escape the effects of climate change (e.g., Magnuson et al. 1997; Jansen and Hesslein 2004; Keller 2007), however the consequences of climate-induced habitat changes for north-temperate fish communities remain poorly understood. The vertical light environment in freshwater lakes affects many important chemical, biological, and physical processes and accordingly plays a vital role in structuring fish community dynamics. Ambient light transmission not only determines the visual environment within which aquatic organisms operate, but also strongly influences lake thermal structure, the availability of appropriate thermal habitat, primary production, and chemical interactions (De Stasio et al. 1996; Magnuson and De Stasio 1996; Jansen and Hesslein 2004). Although increased ambient air temperatures may have a direct impact on thermal structure, the largest influences of climate change on freshwater habitat characteristics will likely be due to altered biogeochemical processes that affect terrestrial inputs of dissolved organic carbon (DOC).

DOC is the primary determinant of water clarity and epilimnion depth in small (< 500 ha), oligotrophic lakes (Fee et al. 1996; Schindler et al. 1997; Keller et al. 2006) typical of those found across north-temperate regions of the boreal forest biome (estimated 98% of lakes in Ontario's Boreal Shield region alone are 1 to 100 ha; Cox 1978). DOC is a complex aggregate of variable organic molecules whose chemical composition and coloured properties are largely determined by its precursor material (McKnight et al. 1994) and the geochemical processes that act on its components (McKnight et al. 1992). DOC can originate both within (autochthonous) and outside of

(allochthonous) lake waters, but it is the allochthonous fraction that is the most highly coloured, owing largely to humic and fulvic compounds that are derived from plant decay in wetlands and forest soils (Cuthbert and del Giorgio 1992; Schindler and Gunn 2003). Higher molecular weight humic fractions in DOC, such as those derived from terrestrial sources, impart higher light absorbance than lower molecular weight fractions (Stewart and Wetzel 1980). Moreover, fulvic acids derived from within-lake microbial processes absorb less visible and ultraviolet light than fulvic acids derived from plant litter and soils because they consist of a lesser proportion of aromatic carbon (12 to 17%) than terrestrially-derived fulvic acids (25 to 30%) (Malcolm 1990; McKnight et al. 1994). The export of highly coloured allochthonous organic material from terrestrial sources often far exceeds the production of autochthonous organic material by primary producers within lakes (Bade et al. 2007). The coloured DOC produced in terrestrial watersheds acts to "stain" lake water and attenuates light through the absorption of solar energy, which in turn affects the heat content of the upper reaches of the water column. Structural variations in DOC molecules also affect the wavelengths of light that DOC absorbs, thus shaping the spectral composition of the light in the water column for primary production and vision. For example, light transmission in humic waters is often narrowed to wavelengths between 500 to 600 nm, which gives these waters its brownish-yellow colour (Pitcher 1993). The large influence that DOC has on lake optical properties and thermal structure thus makes it a primary factor to consider when trying to predict the effect that climate change will have on freshwater fishes (Table A1).

The most important determinant of lake DOC concentrations across much of the northern hemisphere is the proportion of catchment dominated by peatlands, including in Canada's Boreal Plains (Gibson et al. 2002), Canada's Boreal Shield (Dillon and Molot

Table A1. Summary of the main effects that changing DOC concentrations will have on key fish habitat characteristics.

Habitat Characteristic	Direction of change in DOC	
	Increasing	Decreasing
Thermal structure	• shallower thermocline • higher epilimnion temperatures • lower hypolimnion temperatures	• deeper thermocline • increased hypolimnetic heating • possibility of isothermal conditions where stratification usually occurs (especially for clear and shallow lakes)
Oxygen	• depleted in hypolimnion due to prolonged stratification (consumption by respiration) and shorter period of spring mixing	• increased at depth due to greater mixing depths, although warmer temperatures in epilminion hold less dissolved oxygen
Visual clarity	• darker visual environment • less extensive macrophyte cover • shallower UV penetration depths • shallower PAR penetration depths (for primary production) • reduced benthic biomass production	• more illuminated visual environment • more extensive macrophyte cover • deeper UV penetration depths • deeper PAR penetration depths (for primary production) • increased benthic biomass production
Contaminant toxicity	• greater protection against metals and xenobiotic organic pollutants via molecule complexation and physiological changes to gill membrane chemistry	• higher toxicity of metals and greater bioaccumulation of xenobiotic organic pollutants

2005), Scandinavia, and northern Russia (Kortelainen et al. 2006; Sobek et al. 2007). Primary production by terrestrial vegetation appears to be the most important determinant of DOC concentrations in Norwegian boreal lakes, which may be an artefact of Norway's diverse topography (from ocean shore to mountains in a relatively short distance), relatively small proportion of bogs, or the relatively short time for peat accumulation since deglaciation 8000 years ago (Larsen et al. 2011*a*, 2011*b*). Boreal lakes tend to have high DOC concentrations relative to lakes from the arctic or warmer climates due to organic-rich soils that develop from high inputs of litterfall, relatively low microbial decomposition rates in a cool climate, and a large proportion of water-logged soils (Sobek et al. 2007).

Much work has already been done to characterize the potential impacts of climate change on aquatic habitat characteristics, lake metabolism, nutrient cycling, and biotic communities (e.g., see reviews by Magnuson et al. 1997, Keller 2007, and Tranvik et al. 2009), but the task of teasing apart its complexity is ongoing. This paper provides a summary of the current state of knowledge, based on the literature, of the potential effects of climate change on freshwater fish communities in north-temperate regions via changes in ambient light transmission, with special emphasis on the role of DOC in small lakes (< 500 ha). By drawing linkages between the processes that control DOC inputs into lakes and how those inputs affect fish community structure, we seek to aid in making realistic forecasts for climate change effects on these extremely abundant ecosystems.

The majority of examples herein are drawn from Canada's Boreal Shield region, however the findings are applicable to fish communities in similar north-temperate zones across the globe. Although estimated changes in temperature and precipitation over the past decades vary widely across the boreal forest, most areas have become warmer and

wetter (Magnuson et al. 1997; Hengeveld et al. 2005). Climate records over the past 100 years have shown increases in average annual temperatures of 0.6 to 1.4 °C and increases in average annual precipitation of 14 to 21% across three climatic zones of the Boreal Shield (Great Lakes/St. Lawrence, Northwestern Forest, and Northeastern Forest; Magnuson et al. 1997). The largest temperature increases, however, have occurred during the winter and spring seasons with very little change in summer and autumn temperatures. Precipitation increases have occurred mostly in summer and autumn (Magnuson et al. 1997; Hengeveld et al. 2005; Parker et al. 2009). Increases in heavy precipitation events are also forecast to accompany climate warming across Scandinavia, especially during autumn, and the greatest changes in temperature are also forecast to occur in winter (Christensen et al. 1996). Despite variability in the magnitude of predicted future climate change both among models and among regions of the boreal forest, increased temperature and precipitation trends are generally expected to continue (Magnuson et al. 1997; Hengeveld 2004).

OVERVIEW OF PREDICTED CHANGES IN DOC AND LAKE STRUCTURE

Given the strong dependency of water clarity on inputs of terrestrially-derived DOC in small lakes, the greatest impacts of warming temperatures and changing weather patterns on these systems will likely be manifest through indirect changes in watershed processes that affect DOC inputs rather than through the direct effects of changing air temperature (Fee et al. 1996; Snucins and Gunn 2000; Keller 2007). Climate, along with topography, regulates hydrology, soil composition, and land cover, which in turn are the most important controls on DOC inputs to lakes (Benoy et al. 2007; Sobek et al. 2007).

Lake clarity may shift based on complex interactions between rates of decomposition, terrestrial runoff, the existing water chemistry of the lake, shifts in forest community composition in the drainage basin, and changing season lengths.

There has been a general increase in DOC in aquatic systems over the past few decades in eastern North America and large parts of northern and central Europe that can be attributed to both changing weather patterns and widespread recovery from anthropogenic acidification (Driscoll et al. 2003; Miettinen et al. 2005; Monteith et al. 2007; Parker et al. 2009). Some systems have exhibited substantial declines in DOC as a result of changing weather patterns and more frequent extreme drought events (e.g., Schindler et al. 1996; Gunn et al.2001; Parker et al. 2009), but these are often temporary shifts from short-term climatic events that may only last for a few years. Such analyses over shorter time scales can mask long-term trends in biogeochemical processes (Magnuson 2002). While it is important to consider that some systems will experience clearer waters based on local climate and topography, the boreal forest biome as a whole is expected to experience greater DOC loadings in lakes and streams (Benoy et al. 2007). It is important to understand the effects that decreased clarity will have on the availability of thermal habitat, species distributions, competition, predator-prey interactions, biomass production, and physiological stress for freshwater biota. The magnitude of responses to climate change will likely be lake and species specific, but overall changes in broad-scale weather patterns will spur community shifts that create more general and predictable alterations to fish production across the larger landscape (e.g., at the ecozone scale).

Hydrological Effects

Rising temperatures could enhance decomposition rates in wetlands and forest soils and consequently produce more organic material available for export from the watershed (Freeman et al. 2001*a*; Keller 2007), while increased precipitation could enhance DOC export rates (Andersson et al. 1991; Hinton et al. 1997). A greater frequency of short-term drought events could also result in increased mobilization of DOC to lakes where lowered water levels in wetlands prompt oxidation and microbial degradation of previously submerged peat (Freeman et al. 2001*b*). Elevated DOC inputs produce darker lakes with shallower thermoclines and cooler hypolimnia due to a reduction in the depth to which solar energy can penetrate (Fee et al. 1996; Snucins and Gunn 2000). DOC-induced warming of surface waters can also reduce oxygen levels in the hypolimnia of dark lakes by causing lakes to stratify early in the spring before mixing can replenish deep oxygen-depleted waters (Wissel et al. 2003) and by enhancing bacterial respiration (Arvola et al. 1996). In contrast, sustained drought and high evapotranspiration rates can lead to declines of DOC in lakes as a result of reduced export of organic material (Parker et al. 2009). Reduced stream and groundwater flow rates also result in longer lakewater residence times that allow greater time for in-lake photodegradation and mineralization of DOC (Andersson et al. 1991; Pace and Cole 2002; Parker et al. 2009). In contrast, sustained high precipitation rates could also result in decreased DOC export in the long-term if leaching from runoff is not balanced by a high production of organic carbon in soils (Sobek et al. 2007). In a study analyzing factors regulating DOC concentration in > 7500 lakes, Sobek et al. (2007) found that runoff was strongly negatively correlated with lake DOC. Lower DOC export would result in greater water clarity, deeper thermoclines, greater average temperatures, and

decreased thermal habitat for coldwater fish species (Schindler *et al.* 1996; De Stasio et al. 1996). The rate at which DOC is mobilized from peatlands and other catchment or terrestrial environments will depend on the combined effects of local temperature, precipitation, and watershed characteristics for any given lake (Tranvik and Jansson 2002). Watershed-scale increases in DOC mobilization, however, are expected to trump localized factors that inhibit DOC export, resulting in generally darker lakes across the boreal forest biome in response to climate change.

The response of lakes to changing DOC inputs appears to be also partially dependent on their current DOC status. Clear lakes (DOC < 2 mg/L) are especially sensitive to small changes in DOC concentrations relative to dark lakes. Even relatively small changes in DOC can cause drastic differences in the extent of hypolimnetic heating, light penetration, and thermal structure in very clear lakes (Gunn et al. 2001), which has consequences for primary production, predator-prey dynamics, and habitat availability for aquatic biota. Similarly, lakes with strong hydrological connections to the drainage system (i.e., lakes with prominent outlets and shorter water residence times) are more responsive to changes in DOC inputs on shorter time frames (Pace and Cole 2002). These ultra clear lakes and fast-flushing lakes may represent important study systems for understanding how large changes in water clarity will alter lake environments in the future.

Influence of Changing Plant Communities

Climate not only affects hydrological processes in the drainage basin, but also the forest plant communities that feed into those processes. Longer growing seasons and greater annual terrestrial primary production will likely boost humus accumulation in the

upper soil horizons, thereby increasing the potential for later DOC mobilization (Tranvik et al. 2009; Weyhenmeyer and Karlsson 2009). Moreover, climatic shifts will facilitate the redistribution of plant species (Koca et al. 2006) whose rates of primary production and leaf litter lability (i.e., how easily it breaks down) can affect the quality and quantity of DOC produced by the forest ecosystem (Tranvik et al. 2009). For example, DOC fluxes to temperate forest streams can be 2-4 times greater in watersheds dominated by deciduous vegetation compared to coniferous vegetation, with marked differences in the isotopic composition of organic matter in soil runoff due in part to slower decomposition of coniferous litter (Amiotte-suchet et al. 2007). The northward migration of deciduous forests associated with a warmer climate (Koca et al. 2006) could thus contribute to elevated DOC concentrations in streams and lakes across the northern hemisphere. This may be especially important in areas such as Norway, where terrestrial vegetation appears to be the most important determinant of DOC fluxes. Larsen et al. (2011*b*) found that an index of change in terrestrial vegetation composition (normalized difference vegetation index, NDVI) increased significantly with temperature and precipitation, and that NDVI was the most important predictor of total organic carbon (TOC) in 1000 Norwegian lakes. The model predicted a 65% increase in median lake TOC (to 3.3 mg C L^{-1}) over the next 100 years under an intermediate increase in greenhouse gases.

The extent and severity of forest fires are also expected to increase as the climate warms across much of the boreal regions of Canada and Russia (Stocks et al. 1998), although some regions such as eastern Canada are predicted to experience a decrease in fire danger (Flannigan et al. 2001). The loss of trees in forested catchments (from fire or harvesting) increases groundwater discharge due to reduced evapotranspiration, and the resulting elevated water table can cause greater DOC export as a larger portion of the

groundwater flow bypasses DOC-absorbing mineral soils (Hinton et al. 1997). Lakes in fire-impacted catchments can thus experience significant increases in DOC loadings for several years following fire, along with significant decreases in the depth to which photosynthetically active radiation can penetrate the water column (Carignan et al. 2000). The effects of fire on DOC export may not be seen immediately after the fire, however, since much of the rich organic material in the upper soil horizons is often combusted (MacLean et al. 1983) and charcoal left on the forest floor may absorb a fraction of the DOC (Wardle et al. 1998).

Snowmelt and Ice-Out Effects

Aside from the direct impacts of watershed processes, altered standing stocks of DOC in lakes could be caused by changes in both the timing of spring ice-out and the volume of snowmelt inputs. Long-term trends for later freeze dates, earlier ice-out dates, and shorter durations of ice cover have been observed across the northern hemisphere (Magnuson et al. 2000). The flush of water from spring snowmelt is usually enriched in highly coloured organic matter and can flood nearby streams and wetlands, leading to a marked springtime spike in lake DOC concentrations (Pace and Cole 2002). However, in a study in the Laurentian Great Lakes region earlier ice-out dates were often associated with shallower average snow depths over the winter period (Jensen et al. 2007), resulting in smaller spring freshets that dampen the effect of the spring spike in DOC. Pace and Cole (2002) also observed lower spring DOC concentrations in years with early ice-out dates for 20 lakes in northern Michigan. These authors speculated that DOC accumulated under the ice during winter when it was protected from photodegradation losses, and that shorter ice-covered seasons could reduce spring DOC concentrations, which then has

implications for the establishment of lake thermal structure. Potential declines in DOC from snowmelt and sub-ice accumulation, however, may be of little consequence if DOC inputs are subsequently elevated after ice-out from warmer, wetter spring conditions if precipitation increases as many models predict.

Ultimately, long-term changes in DOC concentrations in lakes will be a result of complex interactions between watershed processes, chemical deposition, and weather patterns (Figure A1; Zhang et al. 2010). Considering the widespread consensus that DOC loading in boreal lakes will generally increase, there is clearly a need for long-term monitoring programs to assess the effects of climate change on water transparency. For instance, an increase of 1.6° C in air and lake temperatures over a 20 year period (1970-1990) at the Experimental Lakes Area of northwestern Ontario was initially associated with lower DOC concentrations (Schindler et al. 1990, Schindler et al. 1996). However, a second analysis with 16 more years of data from the same area (1970-2005) revealed that reductions in DOC export from the surrounding catchment had reversed and had been a result of a prolonged period of drought rather than a direct effect of warming temperatures (Parker et al. 2009). In comparison, a long term continuous record of lakes near Sudbury in northeastern Ontario and lakes near Dorset in south-central Ontario revealed an increase in DOC concentrations over a similar time period (1970-2003) and a similar increase in air temperature (1.1° C; Somers 2006; Keller 2007). Despite apparent variability in the magnitude of water darkening in response to climate change at large landscape scales, intra- and interannual variation in DOC and colour can often be

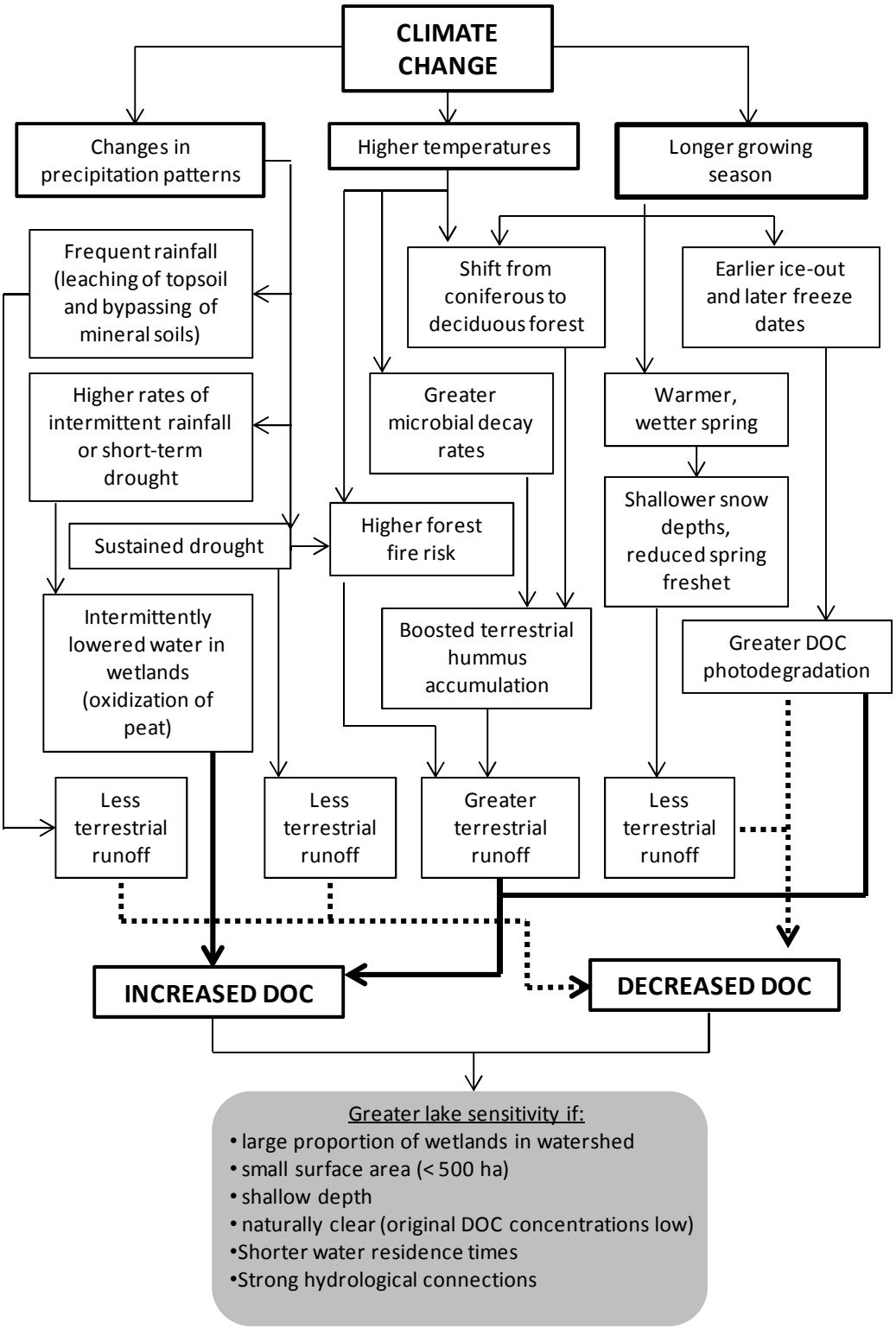

Figure A1. Potential pathways for climate change to cause increased or decreased DOC loadings in lakes through its effects on biogeochemical processes in the watershed, along with lake characteristics that are likely to render a lake more sensitive to altered DOC inputs.

synchronous among lakes at smaller spatial scales (< 3000 ha) due to allochthonous DOC inputs from common headwaters and wetlands (Pace and Cole 2002). Thus, long term predictions of the magnitude of climate change impacts on aquatic systems will likely be most accurate if considered at smaller geographic scales where lakes are not only exposed to similar weather patterns (including precipitation), but also to similar biogeochemistry and watershed characteristics (i.e., soil types, forest composition, and wetland area).

THERMAL HABITAT AND OXYGEN AVAILABILITY

Perhaps the most ubiquitous effect of climate-induced changes in DOC inputs to lakes will be altered thermal structures in the receiving lakes. By attenuating light, DOC plays an important role in controlling the depth to which solar radiant energy can penetrate the water column, thus exerting a strong influence on thermocline depth and epilimnion temperature during summer stratification in dimictic lakes (Fee et al. 1996; Schindler and Gunn 2003). The most direct link that thermocline depth has to fish assemblages is the determination of optimal thermal habitat volume (Christie and Regier 1988). Fish are ectothermic organisms adapted to optimize physiological processes in particular ambient temperatures, and will actively seek areas of species-specific preferred temperatures within their environment (Fry 1947; Magnuson and De Stasio 1996). In the north-temperate regions of the United States and Canada, fish are generally classified into three laboratory-derived thermal guilds: warmwater (temperature preference centred around 28°C; e.g., most centrarchids), coolwater (24°C; e.g., most percids), and coldwater (15°C; e.g., most salmonids) (Hokanson 1977; Magnuson et al. 1979). Growth and survival are also dependent on oxygen concentrations, which are linked to water

temperature and the establishment of the thermocline depth. Changes in thermal properties from increased DOC inputs thus have consequences for fish communities via both direct temperature effects on growth and reproduction, as well as through the availability of well-oxygenated habitat. While it is often thought that warmer air temperatures will lead to decreased habitat for coldwater species by warming the water column, current models and field observations suggest that the darkening of lake waters will usually mitigate this effect and instead lead to greater coldwater habitat volume and cooler hypolimnion temperatures despite warmer epilimnia (Snucins and Gunn 2000). de Stasio et al. (1996) and Magnuson and de Stasio (1996) used global circulation model (GCM) scenarios to simulate responses of lake thermal regimes to climate change and found that thermal habitat volume (measured as both the available space within a preferred temperature range and the duration of the growing season with suitable temperatures) actually increased for all three thermal guilds in deep, thermally stratified lakes. Thermocline depths also became shallower as light attenuation increased. Models may also underestimate beneficial effects for the various thermal guilds, including coldwater species such as lake trout because they do not usually account for the benefits that slightly warmer water in the epilimnion may provide through increased "scope for activity" (Fry 1949), although there are obvious limits, both physiological and behavioural that cannot be exceeded.

There are, of course, situations where darker lakes will not impart the benefits of thermal volume expansion predicted by GCM models. These models assume that while warm- and coolwater species enjoy habitat expansion from greater epilimnion thicknesses and temperatures, coldwater fish will have the ability to move deeper into cool hypolimnetic waters whose temperatures in seasonally stratified lakes are determined by

spring turnover conditions and thus remain unaffected by water clarity (Stefan et al. 1996). However, deeper waters are often not available in small lakes and even if they are, prolonged periods of stratification can prolong the period of oxygen depletion and food limitation for coolwater predators when pelagic prey species are not present. In very clear or shallow lakes small changes in DOC concentrations can have a large impact on thermal and optical properties (Snucins and Gunn 2000). Gunn et al. (2001) documented significant hypolimnetic heating in some north-temperate ultraclear (DOC < 1.0 mg/L) lakes during the unusually warm summers of 1998 and 1999. For example temperatures were isothermal at 22°C throughout the water column of an 18 m deep lake that usually experiences summer stratification, and lake bottom temperatures in another lake reached 10.1°C at a depth of 54.5 m. The potential for loss of coldwater species (e.g., lake trout) in small clear shallow lakes may not be very severe across much of Canada's southern Boreal Shield region because such lakes are very rare (< 5%; Gunn and Pitblado 2004), but is still of concern for localized extirpations of sensitive populations, especially where short-term drought events temporarily decrease DOC loading.

The benefits of expanded coldwater habitat volume with increasing DOC (via shallower thermoclines) must also be considered in light of the costs incurred by greater anoxia from prolonged summer stratification (Stefan et al. 1996; Magnuson et al. 1997). In lakes where anoxia prohibits habitation by fish, coldwater species will not be able to remain within deep thermal refugia and may be forced to endure the energetic costs of making frequent forays into suboptimal thermal, but well-oxygenated, habitat (Pothoven et al. 2009; Roberts et al. 2009; Brandt et al. 2011). GCM simulations that incorporated a variety of lake depths indicated that a loss of well-oxygenated coldwater habitat occurred

across lakes of all depths, but was especially pronounced in shallow lakes (Stefan et al. 1995). Indeed, well-oxygenated coldwater habitat did decrease from 1970 to 1990 in the Experimental Lakes Area of northwestern Ontario following drought-induced DOC declines (Schindler et al. 1996; Jansen and Hesslein 2004; Parker et al. 2009). The presence of coldwater habitat other than the hypolimnion is thus especially important for the survival of coldwater species in shallow and anoxic lakes, or where frequent drought may occur. For example, Snucins and Gunn (1995) reported the unusual existence of a lake trout population in a shallow isothermal lake where survival was only made possible by the use of very shallow (< 0.5 m deep) groundwater seepage areas that provided a cold thermal refuge. Thermal refugia are also important during extreme climatic heating events, such as El Niño. Gullrock Lake in north-central Ontario, which is isothermal throughout the open water season, experienced unusually high water temperatures during a 1998 El Niño event (Gunn 2002). Bottom temperatures in Gullrock Lake approached lethal limits for lake trout (near 23°C), which resulted in the loss of all hatchery-reared juveniles that had been released earlier that year and forced adults to utilize thermal refugia that appeared to be created by cold groundwater seepage.

Sudden changes in the temperature and oxygen profiles associated with water clarity can cause dramatic changes to fish assemblages in relatively short time periods. For instance, an unexpected change in hydrology following the installation of an experimental curtain across a small, deep lake in Wisconsin caused DOC concentrations in the separated basin to almost double within two years, accompanied by a lowered pH, a shallower thermocline, and a reduced oxygenated layer (Christensen et al. 1996). After separation by the curtain, fish abundance in the darkened acidic basin was considerably

reduced to the point where quantitative abundance measurements were not possible due to low catch per unit effort and low recapture rates.

The availability of appropriate thermal habitat has consequences for fish growth and productive capacity (Christie and Regier 1988). King et al. (1999) found that thermal stratification characteristics explained 44% of the variation in growth for smallmouth bass (*Micropetrus dolomieu*; warmwater), yellow perch (*Perca flavescens*; coolwater), rainbow smelt (*Osmerus mordax*; coolwater), and lake trout (*Salvelinus namaycush*; coldwater) in two lakes in Central Ontario. Casselman (2002) also found that increases in summer and early winter water temperatures had profound impacts on several common freshwater fish in Lake Ontario, one of the Laurentian Great Lakes. Year-class strength was positively correlated with summer temperatures for warmwater smallmouth bass, while year-class strength for coolwater northern pike (*Esox lucius*), coolwater alewife (*Alosa pseudoharengus*, an important forage fish), and coldwater lake trout was negatively correlated with summer and fall water temperatures. For lake trout, particularly, an increase of 3° C during fall spawning (after turnover, when the hypolimnion no longer exists) could cause a 20x decrease in survival at hatch for lake trout embryos (Casselman 2002). Changes in thermal volumes through changes in water clarity could thus alter the distributions and relative abundances of fish species with differing thermal optima and upper incipient lethal limits.

It is important to note that some among-population variation in upper incipient lethal limits can occur due to acclimation and phenotypic plasticity (Fry 1947) which may mitigate large or rapid community shifts in some cases. Observations of electronically tagged lake trout in a central Ontario lake without pelagic prey fish revealed that feeding

forays into warmer littoral areas exceeding their physiological temperature optimum were frequent (Morbey et al. 2006). Moreover, the frequency of forays was highly variable among individuals suggesting that some individuals were more tolerant of warm temperatures than others. Galarowicz and Wahl (2002) also observed that concordance between life history characteristics and climatic conditions in walleye populations across North America differed between geographic zones that had been colonized from differing glacial refugia. These results suggest walleye adaptation to climatic conditions had been a result of evolutionary divergence since the last glaciation, and provide evidence for genetic variability among populations that could aid in walleye resilience in the face of a changing climate.

Over time, changes in thermal and oxygenated habitat volume could simultaneously lead to the localized extirpation of prominent coldwater species such as lake trout and brook trout (*Salvelinus fontinalis*) (Shuter and Post 1990; Chu et al. 2005). Similar fates are forecast for north-temperate stream fish populations where cold water thermal refugia will likely only occur in areas with substantial groundwater inflows or at high elevation headwaters (Eaton and Scheller 1996), heightening concerns about the health of fragmented populations as coldwater species form isolated "pockets" across the landscape (Rahel 2002).

RANGE EXPANSION

Although fish must seek suitable habitat within the confines of their respective lakes and streams, warming temperatures will facilitate distributional range shifts as previously uninhabitable waters become suitable at northern limits, and previously suitable waters become uninhabitable at southern limits. Regional variation in secondary

watershed lake characteristics is better predicted by ecozone than by primary watershed (Minns et al. 2008), suggesting that shifts in ecozone boundaries in response to climate will also alter lake typologies. These changes will likely happen faster along the northern boundary of the boreal forest biome where previously subarctic lakes may become north-temperate (e.g., summer stratification will become increasingly common and maximum summer temperatures will increase; Edmundson and Mazumder 2002). Enhanced DOC loading could hasten these transformations in lake typology. In a study of 60 Alaskan lakes, Edmundson and Mazumder (2002) found that stained lakes had longer growing seasons and higher maximum water temperatures (by 3° C) than clear or glacial lakes, and that the length of growing season showed a strong latitudinal gradient even within a latitudinal range of only 10°. Taken together, these results suggest that transitioning lakes along the boundaries of shifting ecozones will be dynamic areas of fish adaptation, extirpation, and invasion and thus present important sites for establishing long-term monitoring programs aimed at understanding species resilience in the face of climate change and greater DOC loadings.

North-temperate waters generally experience annual cycles of resource abundance during warm ice-free seasons, and resource scarcity during cold, ice-covered seasons (Shuter and Post 1990). Species distributions, such as those for coolwater yellow perch and warmwater bass, are often limited by the ability of juvenile fish to reach a sufficient size during the growing season to avoid starvation during winter (Shuter and Post 1990; Jackson and Mandrak 2002). Warming temperatures and a longer growing season will likely release populations currently at their northern limit from resource restrictions, and could permit range expansions on a scale of hundreds of kilometres (Shuter and Post

1990; Minns and Moore 1995; Chu et al. 2005) with potentially severe consequences on native fish communities (Vander Zanden et al. 1999; Jackson and Mandrak 2002). Climate warming simulations performed by Minns and Moore (1995) predicted that species richness in lakes across Ontario would increase by three new species on average. Changes in community dynamics from three additional species could be drastic (Magnuson et al. 1997). Moreover, the altered water clarity conditions that occur simultaneously could act to shift the competitive balance among visual foragers so that native fish assemblages become either more or less resilient against invasions.

Native warmwater fish that move northwards could effectively act as invasive species where they detrimentally impact native coldwater communities. Such is the case for the impact of smallmouth bass on brook trout and lake trout. Invading smallmouth bass act as voracious littoral predators that substantially reduce the amount of littoral forage fish available to native trout (Vander Zanden et al. 1999). Smallmouth bass introductions have been associated with lake trout population declines of about 70% across northern Ontario (Lepak et al. 2006; Kaufman et al. 2009). Moreover, Jackson and Mandrak (2002) predicted that more than 25 000 cyprinid populations in Ontario alone may be extirpated as a result of smallmouth bass invasions by the year 2100 as warming waters allow greater overwinter survival, which could have drastic trophic consequences for native predators that rely on cyprinid prey. The model did not include water clarity as a predictive variable, but it is possible that darker waters could affect smallmouth bass impacts through shifts in feeding behaviour and consumption rates (Carter et al. 2010).

Anthropogenic introductions could expand species ranges at a much faster rate than would otherwise occur naturally (e.g., Scott and Crossman 1973), especially where plasticity in thermal tolerance allows a species to survive in habitats just slightly outside

of their preferred conditions. Smallmouth bass populations in northern Ontario are also an excellent example of this, where the proliferation of smallmouth bass can be linked to anthropogenic stocking of lakes along major railways in the early 1900's (Lasenby and Kerr 2000). Smallmouth bass are generally considered a warmwater species whose northern range was historically restricted to the Laurentian Great Lakes (Scott and Crossman 1973). Anthropogenic introductions have now established populations as far north as Yellowknife in the Northwest Territories, Canada (W. Keller 2011; personal communication).

While the idea of a natural distributional range shift may at first sound like a gradual process as warmwater species outcompete coldwater species at southern range limits, extreme heat shock mortality events can also occur that would help facilitate domination by warmwater invaders. For instance, unusually warm summer temperatures in 2001 caused the first recorded stratification event in Hawley Lake of the Hudson Bay Lowlands in northern Ontario, resulting in surface temperatures upwards of 20º C that corresponded with major die-offs of sea-run brook trout and common white suckers (*Catostomus commersoni*) downstream of Hawley Lake in the Sutton River (Gunn and Snucins 2010). Similarly, Atlantic salmon (*Salmo salar*) populations in the Miramichi River in New Brunswick, Canada commonly experience severe heat stress during the summer and any further increases in river temperatures due to climate change could pose a large risk to the population, which is currently one of the most productive in Canada (Lund et al. 2002).

THE VISUAL LIGHT ENVIRONMENT

Predictions about species movements based on thermal regimes assume that fish are able to thrive in their optimal temperatures regardless of the visual light environment. However, habitats are multidimensional, and the effect of one environmental variable can "mask" the effect of another (Fry 1947). Temperatures can vary substantially even at a given level of water clarity, especially across geographic ranges. This means that a species' success will depend on its ability to thrive both within a given temperature range and within a range of ambient light conditions. Light transmission usually has a strong negative exponential correlation with DOC concentrations in oligotrophic lakes (Fee et al. 1996; Keller et al. 2006; Karlsson et al. 2009) Thus altered DOC inputs will have a large influence on the visual environment within which fishes must operate. Lowered light intensities could alter competition and predator-prey interactions at all levels of the food chain through various mechanisms, including the visual detection of predators and prey, foraging efficiency, the presence of vegetative cover for ambushing prey or taking refuge, and inhibited benthic and primary production at the bottom of the food web that support higher trophic levels.

Fish Vision and Foraging Strategies

Many of the top piscivorous predators in north-temperate lakes rely to some degree on the visual detection of prey. Visual reaction distances of fish to predators or prey is based on characteristics such as size and contrast with the background, as well as on water clarity parameters such as light intensity and turbidity (Aksnes and Utne 1997; Utne-Palme 2002; Carter et al. 2010). Under water vision is impaired by light scatter (largely due to suspended particles) and absorption (largely due to coloured organic

matter and phytoplankton), resulting in low light intensity and poor image transmission (Aksnes and Utne 1997). Turbid waters restrict the range of a fish's vision because there are more particles to scatter and absorb light between the object and the fish's eye, which results in a lesser degree of contrast between the object and the background (Pitcher 1993). Optimal light intensities for visual foraging differ among species depending on characteristics of eye physiology such as the size and distribution of rods and cones, retinomotor responses, presence or absence of reflective material, and concentration of melanin (Ali et a. 1977). For instance, in laboratory experiments maximum reaction distance to prey fish occurred around 3340 lux for largemouth bass (*Micropterus salmoides*; Howick and O'Brien 1983), corresponding to relatively high ambient light intensities in shallow waters, whereas maximum reaction distances occurred around 17.8 lux for lake trout, corresponding to relatively low ambient light intensities at 10 to 40 m in mesotrophic lakes (Vogel and Beauchamp 1999). Optimal light conditions can also differ between life stages of the same species as eye physiology changes and ontogenetic shifts in foraging strategies occur (Hairston et al. 1982; Bulkowski and Meade 1983)

Consequently, shifts in feeding behaviours could occur as a result of decreasing water clarity conditions as fish adapt to suboptimal foraging conditions. Carter et al. (2010) demonstrated that smallmouth bass shifted from selectively feeding on a benthic prey fish in clear water to showing no preference between benthic prey fish, pelagic prey fish, and crayfish in turbid waters. Moreover, overall consumption rates declined with decreasing light intensity (Carter et al. 2010). Lake trout habitat selection under the darkness of ice cover also illustrates the importance of ambient light conditions for fish behaviour. In winter, lake trout have been shown to mostly occupy the upper 3 m of the water column in the central region of the lake, where snow depth is generally lower and

low-angle sunlight generally endures longer than at nearshore areas (Blanchfield et al. 2009). This is a vast contrast to their generally wide distribution in deep waters during summer, and occurs despite little evidence that prey fish congregate in the same regions (Blanchfield et al. 2009). Populations of species ill-adapted to low light conditions may decline as DOC inputs rise. Model projections indicated that climate-related reductions in water clarity could cause a 49% reduction in growth rate for Chinook salmon (*Oncorhynchus tshawytscha*) by 2030 due to lower prey encounter rates in darker lake waters (Brandt et al. 2002). There is also some evidence that prey fish defences against predators are reduced in low subsurface illumination, including shorter reaction distances (Howick and O'Brien 1983) and less coordinated schooling abilities (Vandenbyllaardt et al. 1991).

In contrast, some predators are likely to be more successful in darker waters due to special adaptations to low light intensities. One of the best examples of such an adaptation is the specialized eye structure of the walleye (*Sander vitreus)*. In adult walleye, the tapetum lucidum and macroreceptors enhance low-light vision by reflecting light back onto the photoreceptors, contributing to walleye's ability to forage more efficiently in dark waters where they have the visual advantage over prey (Ryder 1977; Vandenbyllaardt et al. 1991). This enhanced sensitivity to light is the most important factor controlling walleye behaviour, causing them to minimize activity during the day and restrict feeding to nocturnal and crepuscular periods in clear waters (Ali et al. 1977). Indeed, walleye abundance appears to be negatively correlated with water clarity parameters (Ferguson 2004). Northern pike (*Esox lucius*), which are commonly found in sympatry with walleye, are also effective hunters in low light intensities due to well-developed vision and lateral lines (Volkova 1973; Dobler 1977), although increases in

pike condition with water clarity have been documented in Canadian prairie lakes, along with improved feeding efficiency under the clearer water conditions that accompany ice formation in the fall (Craig and Babaluk 1989). In central Scandinavia, aggressive brown trout (*Salmo trutta*) tend to dominate the littoral zone of inland lakes during the summer and force sympatric arctic char (*Salvelinus alpinus*) to use less optimal resources (Langeland et al. 1991). However arctic char are a stronger competitor than brown trout in dark waters (Helland et al. 2011), resulting in cohabitation of the littoral zone under the cover of ice, and a higher impact of arctic char on brown trout consumption rates in winter and in dark lakes (Ulvan et al. 2012). Earlier ice out dates in a warming climate can thus alter seasonal competitive interactions between brown trout and arctic charr, although the predicted increases in DOC runoff may mitigate some of this effect (Ulvan et al. 2012).

For planktivorous fishes it is expected that the greatest impacts of increasing DOC will be decreased visual acuity (Vinyard and O'Brien 1976; Diehl 1988; Link and Edsall 1996; Bramm et al. 2009) and shifts in zooplankton behaviour (De Stasio et al. 1996; Wissel et al. 2003). Many zooplankton exhibit diel vertical migration whereby they take refuge from visual predators in the dark, often anoxic hypolimnia during the day and migrate to surface waters to feed at night (Ringelberg 1999). In high-DOC lakes, the amplitude of migration is greatly reduced since the metalimnion and epilimnion are dark enough to provide refuge from visual planktivores but do not incur the same costs on growth and reproduction as the cold temperatures of the hypolimnion (Wissel et al. 2003). Elevated DOC concentrations and epilimnion temperatures could result in a shallower daytime position of zooplankton without additional predation risk since decreased clarity greatly interferes with the efficiency of planktivory by fish (De Stasio et al. 1996; Wissel

et al. 2003). Changes in the vertical distribution of both zooplankton and fish would likely result in greater overlap between predator and prey for warmwater planktivores that experience an expansion of available thermal habitat volume, although some zooplankton would be forced into the less optimal hypolimnion as a result (De Stasio et al. 1996). Predator-prey overlap for coldwater planktivores would decrease as fish move into deeper, colder waters and zooplankton occupy warm surface waters (De Stasio et al. 1996).

Among the common large-bodied piscivores and benthivores native to north-temperate lakes, smallmouth bass, largemouth bass, lake trout, burbot (*Lota lota)*, and lake whitefish (*Coregonus clupeaformis*) tend to be more abundant in lakes with relatively higher water clarity (Howick and O'Brien 1983; Marshall and Ryan 1987; Vogel and Beauchamp 1999; Carter et al. 2010), whereas walleye, northern pike, common white sucker, and yellow perch tend to be more abundant in lakes with relatively lower water clarity (Volkova 1973; Marshall and Ryan 1987; Margeneau et al. 1998; Ferguson 2004; Lester et al. 2004). Changes in feeding success and prey preferences linked to an altered visual environment have the potential to cause shifts in competitive balances that could cause top-down cascades throughout the food web and ultimately incur dramatic changes to community structure.

Macrophyte Cover

Macrophyte cover, the density of which is controlled by light transmission through the water column, is an important habitat structure for both predator and prey fish species. Sit-and-wait predators such as northern pike rely on submerged vegetation to ambush prey as adults, to act as cover against predation as juveniles, and for spawning

habitat (Casselman and Lewis 1996; Skov et al. 2002). Littoral forage fish often use macrophytes as a refuge from predation. Elevated DOC concentrations under a warmer, wetter climate have the potential to substantially reduce the extent of macrophyte cover (Squires et al. 2002), which could translate to lower fish production for those species that rely on macrophytic habitat. Changes in macrophyte species composition in response to changing light conditions could also have trophic consequences for how fish and invertebrate prey use basal resources. Stable isotope analyses revealed wider trophic niches (greater spread along the $\delta^{13}C$ axis, corresponding to a wider array of dietary carbon sources at the population level) for fish and benthic invertebrates in lakes dominated by invasive Eurasian milfoil (*Myriophyllum spicatum*) versus lakes dominated by native macrophytes (Kovalenko and Dibble 2011).

Production and Trophic Transfers

Allochthonous DOC plays a major role in production at the base of the food web in nutrient-poor lakes typical of those in the boreal forest through two mechanisms – by controlling the depth to which photosynthetically active radiation (PAR) can penetrate and by acting as a source of energy for bacterial and zooplankton production. The enhanced DOC loadings forecast for the boreal region may thus exert a strong bottom-up influence on fish production at higher trophic levels (Karlsson et al. 2009). Benthic habitats in oligotrophic north-temperate lakes produce more new biomass than pelagic habitats, except in very deep lakes (Karlsson et al. 2009). Allochthonous organic carbon can directly support this benthic biomass production by acting as a resource for bacterial and heterotrophic production in benthic habitats (Ask et al. 2009; Solomon et al. 2011), and can also support increased zooplankton production in pelagic habitats (Jones et al.

2012). At the same time, high DOC loading acts as a strong inhibitor of benthic primary production through light attenuation, which can have significant trophic consequences. Karlsson et al. (2009) found that light availability in small, oligotrophic lakes controlled fish production via its influence on benthic algae primary production. Increases in fish use of pelagic autochthonous organic carbon did not compensate for the loss of benthic production in dark lakes, indicating that allochthonous DOC was an important limiting nutrient for fish production. Indeed, the diets of north-temperate fishes can comprise > 60% benthic resources (Vander Zanden and Vadeboncoeur 2002). Consequently, terrestrial reliance is higher, and benthic reliance is lower, across all consumer groups in humic lakes compared to clear lakes (Solomon et al. 2011). DOC is thus an important link between benthic, pelagic, and terrestrial food webs and can strongly influence the extent to which consumers use resources from each area (Solomon et al. 2011). Large increases in DOC are expected to enhance the utilization of terrestrial subsidies in aquatic food webs and cause negative impacts on overall fish production across oligotrophic lakes in the boreal forest biome.

Enhanced DOC loadings also have consequences for secondary production through its influence on life-history characteristics of secondary consumers. Temperature and photoperiod cues control the production of overwintering eggs in zooplankton and the timing of their release from dormancy (Hairston 1996; Winder and Schindler 2004). Although dark, warm surface waters may release zooplankton from predation pressure and promote egg development, too much of a temperature increase could cause premature hatching of resting eggs and ultimately lead to a decrease in recruitment and abundance (Chen and Folt 1996; Magnuson et al. 1997). Alternatively, decreased light penetration coupled with warmer water temperatures could result in uncoupled trophic linkages.

Winder and Schindler (2004) found that *Daphnia* species that relied more strongly on light (which is independent of climate) as a hatching cue were unable to adjust to the earlier timing of the spring diatom bloom, which is an important energy source for *Daphnia*. The widening gap between the timing of the spring diatom bloom and the spring *Daphnia* bloom corresponded to a significant decline in *Daphnia* densities in spring and summer (Winder and Schindler 2004). Considering the importance of algae-zooplankton interactions for energy transfers to higher trophic levels (Platt et al. 2003), changes in zooplankton abundance that accompany water clarity changes could also cascade through the food web to detrimentally impact both planktivores and piscivores, especially during critical periods of juvenile development.

PHYSIOLOGICAL STRESS

Aside from the multitude of effects that DOC has on the physical lake environment, it is also a highly interactive part of the chemical environment and confers various physiological benefits on aquatic organisms. Humic substances in DOC interact with other organic chemicals and metals via various means of binding and adsorption, which then indirectly affects the toxicity of these substances to aquatic organisms by altering their bioavailability (reviewed by Haitzer et al. 1998). DOC also acts directly on gill physiology to counteract the negative effects of toxicants (reviewed in Wood et al. 2011). Moreover, DOC is an effective attenuator of ultraviolet radiation (UVR) and can protect aquatic organisms from the harmful effects of UVR when present in high concentrations (Scully and Lean 1994), although the extent of protection is both difficult to quantify and highly variable. Thus DOC, in terms of a chemical rather than a habitat

modifier, will likely confer immunological advantages to north-temperate fish populations as DOC levels rise across the boreal forest biome.

Alterations to Pollutant Toxicity

It is now well accepted that DOC plays an important role in reducing the toxicity of metals and the bioaccumulation of organic pollutants by binding to toxicants to form aggregate molecules that are too large, too polar, or both to cross or bind to the gill membrane (Haitzer et al. 1999; Wood et al. 2011). Indeed, DOC concentration is now incorporated into oft-used models that predict site-specific metal toxicity (e.g., Biotic Ligand Models; Niyogi and Wood 2004). Reduced bioaccumulation in the presence of DOC has been experimentally demonstrated for organic pollutants such as polycyclic aromatic hydrocarbons (PAHs), dehydroabeitic acids (DHAAs), chlorinated hydrocarbons, and other xenobiotic organic pollutants (Haitzer et al. 1998; Haitzer et al. 1999). Reduced toxic effects of metals such as aluminum (which is considered one of the most important toxicants to freshwater biota; Rosseland and Staurnes 1994) on both growth rates and mortality have also been demonstrated for freshwater organisms (e.g., Wilson and Wood 1992; Gundersen et al. 1994). Inorganic monomeric species of Al precipitate on the gills causing respiratory interference and ionoregulatory and osmoregulatory failure. Failure occurs due to increased loss and decreased uptake of biologically important ions (e.g., Na^+, Cl^-, Ca^{2+}), increased membrane permeability, inhibition of uptake mechanisms due to intracellular Al accumulation, and gill lesions (reviewed in Rosseland and Staurnes 1994). The negative impact of inorganic monomeric Al is also compounded as it competes for binding sites on the gill membrane with Ca^{2+}, an essential regulator of the ionic and osmotic balance (Rosseland and Staurnes 1994).

DOC acts as an Al-complexing ligand and thus reduces the availability of toxic monomeric Al species (Rosseland et al. 1990). This is especially important for lakes where DOC is increasing due to recovery from acidification, since acidified waters are often associated with low DOC, low Ca, and elevated monomeric Al (Rosseland et al. 1990).

Although much earlier research focussed on the role of DOC as a ligand to bind and detoxify harmful contaminants, recent studies have revealed that DOC can also act directly on gill physiology to counteract toxic effects on ionoregulation and osmoregulation by affecting gill permeability (reviewed in Wood et al. 2011). The primary mechanism of acute toxicity of many metals (e.g., Cu, Ag) to freshwater biota is the inhibition of active Na^+ uptake and the destabilization of paracellular pathways that increase ion leakage (Niyogi and Wood 2004). Galvez et al. (2009) found that both adult rainbow trout (*Onchorhynchus mykiss*) fitted with catheters on the gills and *in vitro* cultured rainbow trout gill epithelial cells displayed a more negative transepithelial potential (TEP) when exposed to natural organic matter, which would favour active uptake of Na^+ by reducing the opposing electrochemical gradient. Moreover, altered concentration-dependent kinetics of Na^+ uptake have been observed in the presence of DOC for various fish species, stimulating increased Na^+ uptake (Matsuo et al. 2004; Glover et al. 2005). Long-term exposure to elevated DOC concentrations has also been shown to increase the activity of gill Na^+, K^+-ATPase (McGreer et al. 2002), the main enzyme functioning in gill ion transport (Evans et al. 2005). Thus high DOC concentrations are beneficial to pollutant resilience in freshwater biota both by complexation of toxicant molecules and direct physiological alterations to the gill membrane that counteract toxic effects. It is important to note, however, that toxic

thresholds are species and life-history stage-specific (Rosseland and Staurnes 1994) so that the effects of increasing DOC will have varying consequences depending on the resident fish assemblage.

It is the humic fraction (humic and fulvic acids) of DOC that confers the greatest protection against organic and metal pollutants, and thus dark, humic-rich allochthonous DOC has a particularly high protective capacity (Wood et al. 2011; Garvey et al. 1991). The effect of humic substances on contaminant toxicity varies depending on both its concentration and origin, so that DOC from different sources varies in its protective capacity (Landrum et al. 1987; Haitzer et al. 1999). Such variability is related to the spectroscopic and chemical properties of the humic substances. In experiments comparing the effects of humic substances from 7 different sources on the bioaccumulation of organic pollutants, Haitzer et al. (1999) found that 76 to 83% of the variation in bioaccumulation could be attributed to the percentage of aromatic carbons in the humic substance. Additional significant relationships were found with absorptive properties, the atomic H/C ratio, the metal complexing capacity, the molecular weight, and the percentage of phenolic hydroxyl groups. However, optical analysis of DOC generally provides a better indication of its protective capacity than analysis of its chemical properties and components (Wood et al. 2011).

Protection from UVR

DOC is also an effective attenuator of ultraviolet radiation (UVR) and can act to protect aquatic organisms from the negative effects of UVR when it is present in high concentrations (Scully and Lean 1994; Williamson et al. 1999). Declines in DOC export thus have the potential to render aquatic organisms in near-surface waters more

vulnerable to UVR exposure. Yan et al. (1996) observed a three-fold increase in the depth to which UVR could penetrate the water column following a reacidification event that resulted in DOC declines from 190 to 63 μmol C l^{-1}. The consequences of UVR for aquatic biota are poorly understood and appear to be species and habitat specific, but are often associated with mutagenic effects on DNA and interference with biomolecular reactions that alter countless processes within the ecosystem – from photosynthesis to fish larval development (Williamson 1995; Gonçalves et al. 2010).

For plankton, UVR generally has negative effects when considered independently from other environmental factors, but some species of both phytoplankton and zooplankton appear to have varying sensitivities to UVR depending on latitude, temperature, nutrient availability, degree of mixing in the water column, and acclimation to naturally clear waters (Villafañe et al. 2004; reviewed in Gonçalves et al. 2010). Darker lakes could thus enhance photosynthetic efficiency at the base of the food web through UVR protection, but overall primary production rates could still be reduced from decreased penetration of PAR, with uncertain consequences for higher trophic levels (Cabrera et al. 1997; Barbieri et al. 2002; although see Xenopolous and Schindler 2003).

Top-down controls on primary production could also be altered by UVR penetration due to the harmful effects of UVR on both invertebrate and fish predators. Higher inputs of protective DOC from climate change could allow planktivores to increase surface water foraging throughout the day (Williamson et al. 1999) which could shift predator-prey dynamics and result in an increase of primary productivity (via reductions in large zooplankton grazer densities). Elevated UVR exposure has also been linked to impaired embryo and juvenile development in several north-temperate

piscivorous fish species such as northern pike (Vehniäinen et al. 2007) and yellow perch (Boily et al. 2011). Epidermal lesions similar to sunburn have also been observed as a result of UVR exposure in rainbow trout (Kaweewat and Hofer 1997; Sommaruga 2001), common minnow (*Phoxinus phoxinus*), and arctic charr (Kaweewat and Hofer 1997). Elevated DOC concentrations could enhance piscivore fitness by alleviating physiological stress from UVR, with consequences for food web structure.

Research regarding the effects of DOC concentration on UVR exposure for freshwater biota in North American temperate lakes flourished in the 1990's as part of the story of recovery from acidification. Interest has since declined in the northern hemisphere due to high variability in UVR susceptibility and adaptation of both plankton and fish, making the consequences of UVR exposure both difficult to predict and to quantify. Nonetheless, UVR remains an important physiological stressor for aquatic organisms and elevated DOC concentrations predicted across the boreal forest are likely to play a protective and beneficial role for north-temperate fish populations.

SUMMARY AND CONCLUDING THOUGHTS

In summary, elevated DOC concentrations are forecast for most north-temperate lakes as a result of increased temperatures and precipitation under a changing climate, as well as recovery from anthropogenic acidification. The magnitude of changes in DOC runoff, however, will likely be highly variable across the landscape. Declines in DOC may occur in areas that experience less precipitation or more frequent extreme weather events (e.g., drought, El Niño), but these will often be short-term effects and increased DOC inputs are expected to be much more common. Consequent changes in water clarity will affect fish community structure through (1) the availability of optimal thermal and

oxygenated habitat, (2) range expansion for both native and invasive species, (3) altered predator-prey interactions and feeding behaviours from changing visual environments, including altered macrophyte cover, (4) changes in benthic biomass production that cascade to higher trophic levels, (5) physiological stress from exposure to metals, organic pollutants, and UVR penetration, and (6) altered trophic linkages at the base of the food web due to any or a combination of the above factors (Figure A2). Moreover, the influence of DOC-altered habitat on fish assemblages is complicated by the variety of conditions that are required at different stages of growth. Water clarity and associated limnological changes may appear to benefit adults, but may limit the availability of suitable spawning habitat and may restrict recruitment and other aspects of production (Lester et al. 2004). Fish production will respond to water clarity and DOC changes at varying scales across the landscape, making it especially important for fisheries managers to monitor fish populations at a local scale and respond with policies appropriate for their jurisdictions. Limiting human exploitation of stressed populations may contribute to their resilience against climate change (Jackson and Mandrak 2002).

Although climate-induced changes in water clarity are often associated with DOC in small, unproductive lakes typical of the boreal forest biome, it is also important to consider the different responses that may simultaneously occur in different lake types. For instance, wind mixing becomes a more important driver of thermal structure than DOC in large (> 500 ha) lakes with greater fetch (Mazumder and Taylor 1994; Fee et al. 1996). Changes in weather and wind patterns may influence the vertical light environment in lakes by altering the strength of physical mixing and particle resuspension. Climate-induced changes in wind mixing patterns could have equally profound effects on fish habitat and behaviour in large lakes as those changes caused by altered DOC inputs in

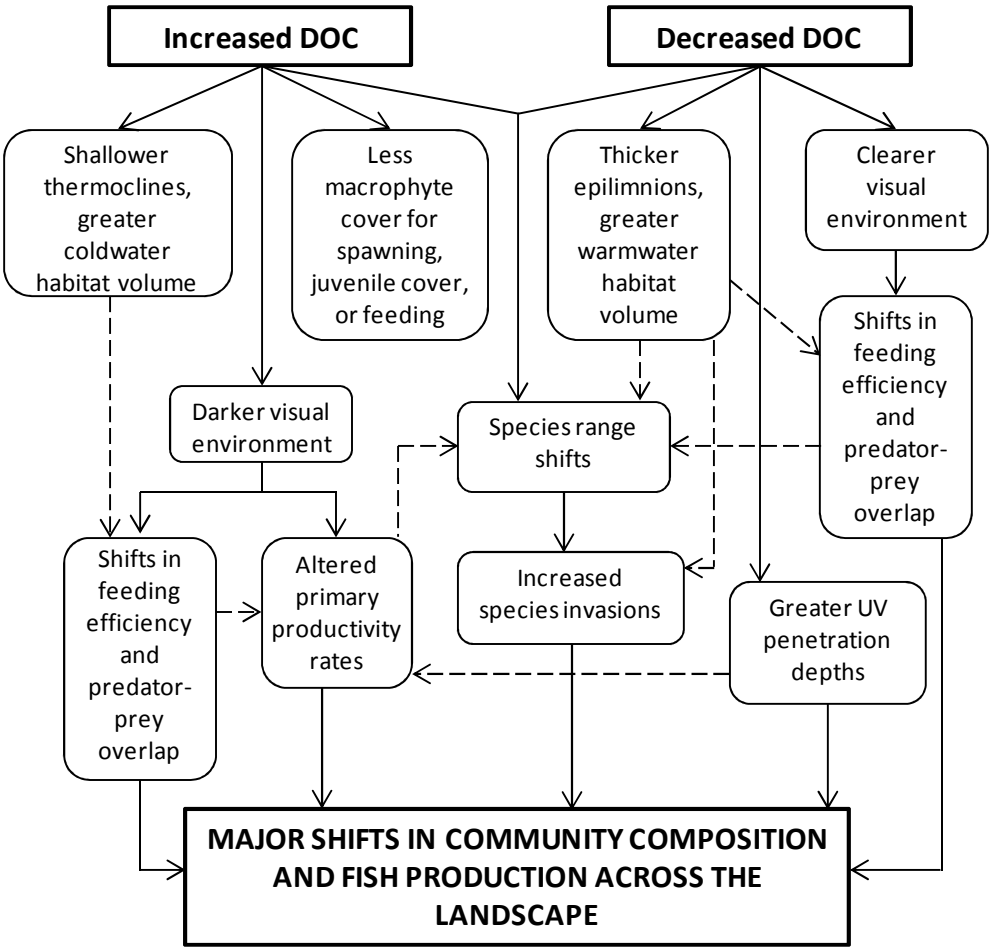

Figure A2. Potential pathways for fish community composition and production to be affected by changes in dissolved organic carbon induced by climate change.

small lakes. Even in small lakes, the effects of climate change could resemble those of eutrophication in agricultural and urban areas due to the increased frequency of pulsed nutrient inflows from flooding and runoff during severe weather events (Magnuson et al. 1997). Although there is little evidence that increased productivity from greater photosynthetic depths will cascade through the food web (Schindler et al. 1990; Magnuson et al. 1997), extended periods of hypolimnetic anoxia associated with longer summer stratification would also promote greater recycling of nutrients from sediments to the water column during spring and autumn mixing events, resulting in algal blooms and eutrophication (Stefan et al. 1996; Magnuson et al. 1997). Eutrophication would have different, albeit equally dramatic, implications for fish communities than would a change in water colour alone (e.g., Tammi et al. 1999; Diaz et al. 2003).

Our understanding of how aquatic ecosystems will respond to major stressors such as climate-induced water clarity changes is steadily improving. Investigations into the complex interactions between climate change, watershed processes, species interactions, and anthropogenic disturbances such as acidification and contaminant deposition have flourished in recent years (e.g., Magnuson et al. 1997; Schindler et al. 1997; Jansen and Hesslein 2004; Keller 2007). Examining the effects of climate change from a multiple stressor perspective is key to making realistic predictions (Keller 2007) and such studies must be drawn upon if we are to advance our understanding of fish responses to the complexities of both subtle and dramatic changes. The majority of our knowledge on DOC impacts has come from observational field studies and so-called natural experiments that test for existing variation in lakes. While these have been extremely informative, there is a need for direct experimental evidence that documents how DOC additions change fish behaviour, production, health, and community composition.

Moreover, although DOC can have both negative and positive impacts on north-temperate fish communities, the elevated DOC concentrations predicted for boreal lakes will still shift key habitat components to which fish must adapt. Much of the current literature refers to shifting DOC concentrations with a relatively neutral perspective, but we propose that elevated DOC concentrations should be viewed as one of the major stressors that will accompany a changing climate in north-temperate lakes.

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APPENDIX B:

Mathematical description of standard ellipses and supplementary R code for calculating SEA_E, NR_E, CR_E, and isotopic overlap of expanded ellipses, and for plotting expanded ellipses in $\delta^{15}N$ vs. $\delta^{13}C$ biplot space.

From Batschelet (1981), the standard ellipse is a bivariate equivalent to standard deviation in univariate data that captures approximately 40% of data points (Batschelet 1981), where the size, shape, and rotation are defined by the covariance matrix associated with x and y, and the location is defined by the means of x and y (centroid at point $\bar{x}, \bar{y}$). The area of the ellipse is then given by πab, where a is the length of the major axis and b is the length of the minor axis, both defined by the covariance matrix.

The standard deviations of x (s_x) and y (s_y), and the correlation coefficient (r) must first be calculated. The standard ellipse can then be constructed within a rectangle centred at ($\bar{x}, \bar{y}$), with sides of length $2s_x$ and $2s_y$ parallel to the x and y axes. The points of tangency, which define the ellipse shape, are drawn at a distance of $\bar{x} \pm r(s_x)$ and $\bar{y} \pm r(s_y)$ (Figure B1). Refer to Batschelet (1981) for further statistical detail in calculating the lengths of the axes and the angle of rotation. These calculations are provided in the SIAR code.

The equation of the standard ellipse can be written as:

$$A(x-\bar{x})^2 + 2B(x-\bar{x})(y-\bar{y}) + C(y-\bar{y})^2 = D$$

where the coefficients are:

$A = s_x^2$

$B = -\text{Cov}(x, y)$

$C = s_y^2$

$D = (1-r^2)s_x^2 s_y^2$

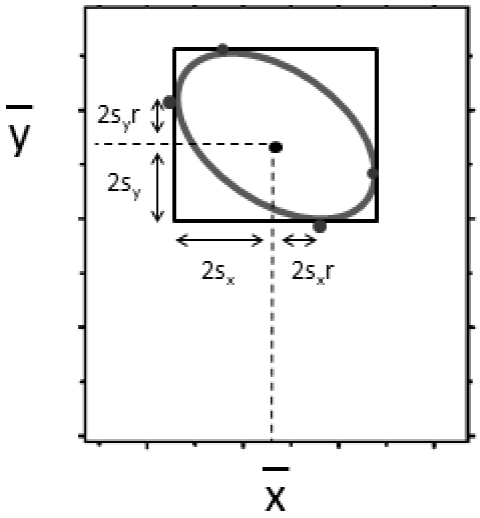

Figure B1. Schematic of the construction of the standard ellipse within a rectangle defined by the means ($\bar{x}, \bar{y}$), standard deviations (s_x, s_y), and correlation coefficient (r) of a set of points. Data points on which variances are based are not shown. Adapted from Batschelet (1981).

The value of D is based on the variances of x and y, the square roots of which are the standard deviations. Thus the standard ellipse captures one standard deviation of the variation in the data points (40% confidence interval approaches 1 SD as $n \rightarrow \infty$). To expand the ellipse to captures a larger number of standard deviations, you must multiply D by the square of the desired number. For example, to expand the ellipse to capture 2

SD, *D* would need to be multiplied by $2^2 = 4$, so $4D$ would result in an ellipse that captured 2 standard deviations of the data.

R Script 1: Expanding ellipses and calculating overlap

The R code below is modified from the siar package (Parnell and Jackson 2011) to expand ellipses to capture a desired number of standard deviations. The specific functions that are modified are `standard.ellipse`, `overlap`, and `plotSigmaEllipse`. It is possible to calculate the ellipse size and dimensions, as well as the overlap between two sympatric ellipses, by simply uploading the ellipse (Murdoch and Chow 2012) and spatstat (Baddeley and Turner 2005) packages, then copy and pasting the functions below into the R console (thus the inclusion of several other, unmodified functions – `hullarea` and `convexhull`). However, reading the original paper (Jackson et al. 2011) and siar package documentation is necessary to understand the inputs required for the functions and for interpretation of the function outputs. It is also recommended so that users understand the full statistical capabilities of siar (for example, calculating the original metrics proposed by Layman et al. (2007) or using Bayesian analyses to calculate ellipses).

```
#First, upload required packages
library(ellipse)
library(spatstat)


#To expand ellipses to capture greater than 1 SD, copy and paste
#the functions below into the R console after uploading the ellipse and
#spatstat packages. Refer to siar package documentation for further
#details and capabilities (such as calculating metrics from Layman et
#al. 2007, Bayesian analyses, etc.)
```

```
#################### standard.ellipse function ####################

#Dmult = the number of standard deviations the ellipse will capture.
#Default of Dmult is 1
standard.ellipse <- function (x,y,confs=NULL,steps=5,Dmult=1){

n <- length(x)

mx <- mean(x)
my <- mean(y)

# ---------------------------------------------------------------------
## Original Parametric methods here
varx <- var(x)
vary <- var(y)

sdx <- sd(x)
sdy <- sd(y)

r <- cov(x,y)/(sdx*sdy)

#Math below taken from Batschelet (1981). Circular Statistics in
#Biology
A <- var(y)
B <- -cov(x,y)
C <- var(x)
D <-(Dmult=(Dmult^2))*((1-r^2)*A*C)

R <- ((A-C)^2 + 4*B^2)^0.5
a <- (2*D/(A+C-R))^0.5
b <- (2*D/(A+C+R))^0.5
theta <- atan(2*B/(A-C-R))

# ---------------------------------------------------------------------
CM <- cov(cbind(x,y))

ac <- a*sqrt((n-1)/(n-2))
bc <- b*sqrt((n-1)/(n-2))

SEA <- pi*a*b

psi <- seq(0,2*pi,steps*pi/180)

# ---------------------------------------------------------------------
# calculate the coordinates of the standard ellipse
xtmp <- mx + a*cos(theta)*cos(psi) - b*sin(theta)*sin(psi)
ytmp <- my + a*sin(theta)*cos(psi) + b*cos(theta)*sin(psi)

tmp <- convexhull(xtmp,ytmp)

xSEA <- tmp$xcoords
ySEA <- tmp$ycoords

# ---------------------------------------------------------------------
# now calculate the coordinates of the sample size corrected ellipse
xtmp <- mx + ac*cos(theta)*cos(psi) - bc*sin(theta)*sin(psi)
ytmp <- my + ac*sin(theta)*cos(psi) + bc*cos(theta)*sin(psi)
```

```
tmp <- convexhull(xtmp,ytmp)

xSEAc <- tmp$xcoords
ySEAc <- tmp$ycoords

# now calculate the confidence ellipse based on the provided levels

xCEA <- NULL
yCEA <- NULL
CEA <- NULL

if (!is.null(confs)){

  CEA <- numeric(length(confs))
  xCEA <- matrix(0,length(psi)+1,length(confs))
  yCEA <- xCEA
  v1 <- 2
  ct <- 0

  for (level in confs){

    ct <- ct + 1

    aCEA <- a * qf(level,v1,n-2)
    bCEA <- b * qf(level,v1,n-2)

    CEA[ct] <- pi * aCEA * bCEA

    xtmp <- mx + aCEA*cos(theta)*cos(psi) - bCEA*sin(theta)*sin(psi)
    ytmp <- my + aCEA*sin(theta)*cos(psi) + bCEA*cos(theta)*sin(psi)

    tmp <- convexhull(xtmp,ytmp)
    xCEA[,ct] <- tmp$xcoords
    yCEA[,ct] <- tmp$ycoords


  }
}

out <- list()
out$CEA <- CEA
out$SEA <- SEA
out$SEAc <- SEA * (n-1)/(n-2)
out$theta <- theta
out$confs <- confs
out$xCEA <- xCEA
out$yCEA <- yCEA
out$xSEA <- xSEA
out$ySEA <- ySEA
out$xSEAc <- xSEAc
out$ySEAc <- ySEAc
out$eccentricity <- sqrt(1-((b^2)/(a^2)))
out$a <- a
out$b <- b
out$r <- r
out$ac <- ac
```

```
out$bc <- bc

return(out)
}

#################### overlap function for standard ellipses ##########

overlap <- function (x1, y1, x2, y2, steps = 5, Dmult=1) {
    E1 <- standard.ellipse(x1, y1, steps = steps, Dmult=Dmult)
    E2 <- standard.ellipse(x2, y2, steps = steps, Dmult=Dmult)
    ex1 <- E1$xSEAc[2:length(E1$xSEAc)]
    ey1 <- E1$ySEAc[2:length(E1$xSEAc)]
    ex2 <- E2$xSEAc[2:length(E2$xSEAc)]
    ey2 <- E2$ySEAc[2:length(E2$xSEAc)]
    e1 <- list(x = ex1, y = ey1)
    e2 <- list(x = ex2, y = ey2)
    out <- list()
    out$overlap <- abs(overlap.xypolygon(e1, e2))
    out$area1 <- abs(E1$SEAc)
    out$area2 <- abs(E2$SEAc)
    return(out)
}


#################### hullarea function (necessary for plotSigmaEllipse)

hullarea<-function (x, y) {
    ne <- length(x)
    harea <- abs(0.5 * ((x[1:(ne - 1)] %*% y[2:ne]) - (y[1:(ne -
        1)] %*% x[2:ne])))
    harea
}

#################### convexhull function (necessary for plotSigmaEllipse)

convexhull<-function (x, y) {
    chI <- chull(x, y)
    chI <- c(chI, chI[1])
    hullX <- x[chI]
    hullY <- y[chI]
    TA <- hullarea(hullX, hullY)
    out <- list()
    out$TA <- TA
    out$xcoords <- hullX
    out$ycoords <- hullY
    out$ind <- chI
    out
}

#################### plotSigmaEllipse function ####################

plotSigmaEllipse <-
function(x,m,sigma,steps=5,Dmult=1,col="black",lwd=1,lty=2){

n <- length(x)

# Extract the coefficients
```

```
A <- sigma[2,2]
C <- sigma[1,1]

B <- -sigma[1,2]

cr <- cov2cor(sigma)

D <-(Dmult=(Dmult^2))*((1-(cr[1,2]^2))*A*C)

R <- sqrt((A-C)^2 + 4*B^2)

theta <- atan(2*B/(A-C-R))

a <- sqrt(2*D/(A+C-R))
b <- sqrt(2*D/(A+C+R))

ac <- a*sqrt((n-1)/(n-2))
bc <- b*sqrt((n-1)/(n-2))

# generate the x,y coordinates of the ellipse


psi <- seq(0,2*pi,steps*pi/180)

xtmp <- m[1] + ac*cos(theta)*cos(psi) - bc*sin(theta)*sin(psi)
ytmp <- m[2] + ac*sin(theta)*cos(psi) + bc*cos(theta)*sin(psi)

tmp <- convexhull(xtmp,ytmp)

xSEA <- tmp$xcoords
ySEA <- tmp$ycoords

lines(xSEA,ySEA,col=col,lwd=lwd,lty=lty)

out <- list()
out$xSEA <- xSEA
out$ySEA <- ySEA
return(out)


}
```

R Script 2: Calculating NR_E and CR_E

The R code below is to calculate the range covered by the ellipse along the $\delta^{15}N$ axis (NR_E), and along the $\delta^{13}C$ axis (CR_E) (See *Methods*). This requires the calculation of the furthest vertical limits of the ellipse along the $\delta^{15}N$ axis (`bottom.N` and `top.N`), as well as the furthest horizontal limits on either side of the ellipse (`left.C` and `right.C`).

These limits can then be used to compute overlap along either individual axis between two sympatric ellipses.

```
#Define population δ15N values as y, and δ13C values as x
#Calculate the mean of x and y
meanC=mean(x)
meanN=mean(y)

#Calculate standard deviations of x and y
#multiply by 2 to get the length of half the ellipse range
#refer to Figure B1)
sd.C=(sd(x))*2
sd.N=(sd(y))*2

#The horizontal limits of the ellipse along the δ13C axis are #then
calculated by adding and subtracting the SD from the #mean
left.C=meanC-sd.C
right.C=meanC+sd.C

#The vertical limits of the ellipse along the δ15N axis are #then
calculated by adding and subtracting the SD from the #mean
bottom.N=meanN-sd.N
top.N=meanN+sd.N

#Calculate the total range along both axes
CR.e=abs(left.C)-abs(right.C)
NR.e=abs(top.N)-abs(bottom.N)
```

APPENDIX C:

Scatterplot matrices of isotopic niche dimension and interaction metrics with habitat and community variables.

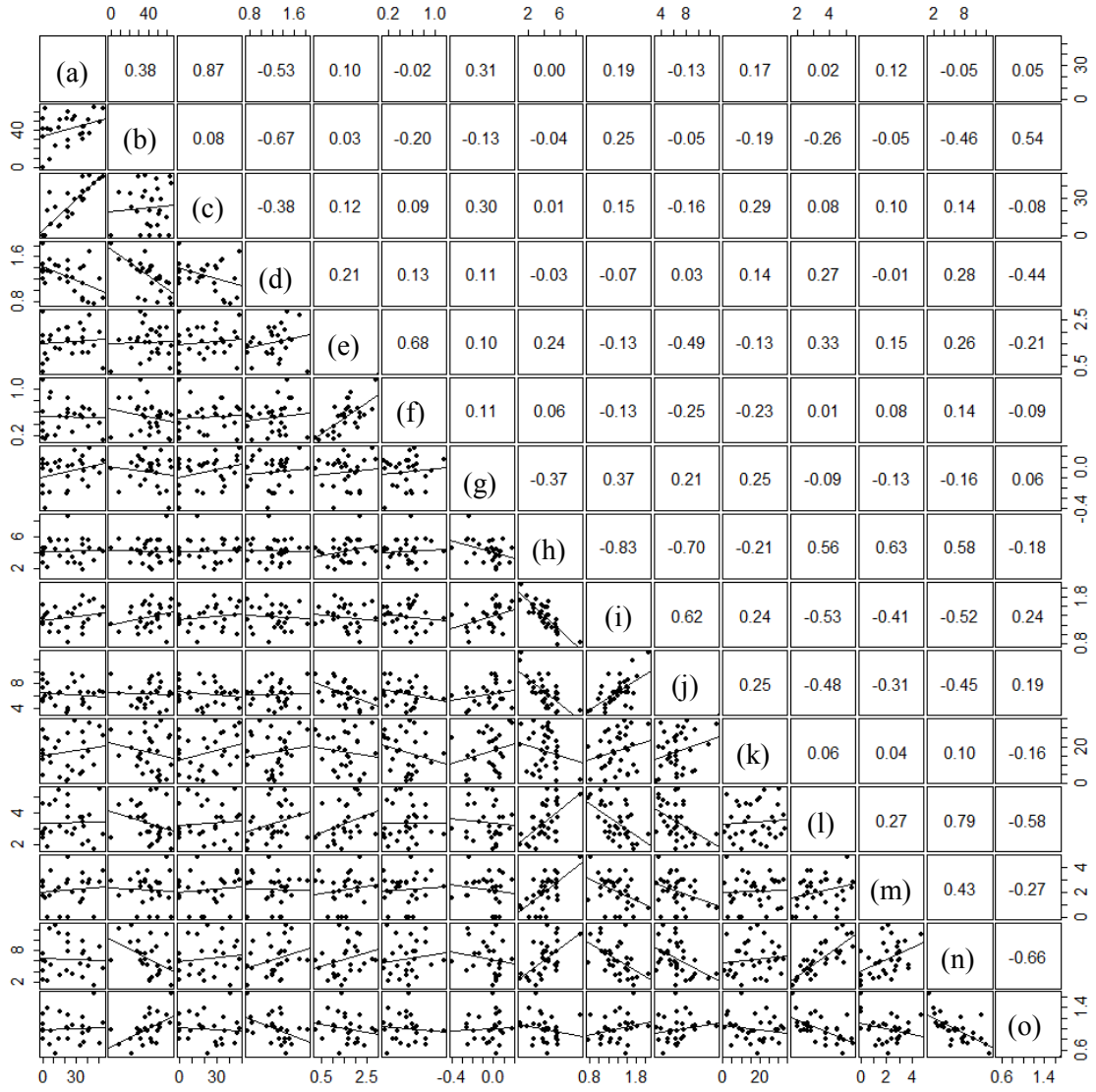

Figure C1. Scatterplot matrix of isotopic interaction metrics: (a) arcsine square-root transformed % isotopic overlap, (b) arcsine square-root-transformed carbon overlap, c) arcsine square-root-transformed nitrogen overlap, (d) square-root-transformed distance between population centroids (DBC), (e) square-root-transformed difference in niche size (SEA_{DIFF}), (f) square-root-transformed absolute difference in trophic diversity (CD_{DIFF}), and (g) square-root-transformed difference in trophic evenness ($SDNND_{DIFF}$); and habitat variables: (h) Secchi depth, (i) $\log_{10}$ true colour, (j) DOC, (k) thermal optical habitat volume for walleye (TOHA), (l) square-root-transformed oxic depth, (m) square-root transformed-anoxic depth, (n) lake mean depth, and (o) $\log_{10}$ morpho-edaphic index (MEI). Correlation coefficients are reported in the corresponding box of the upper panels.

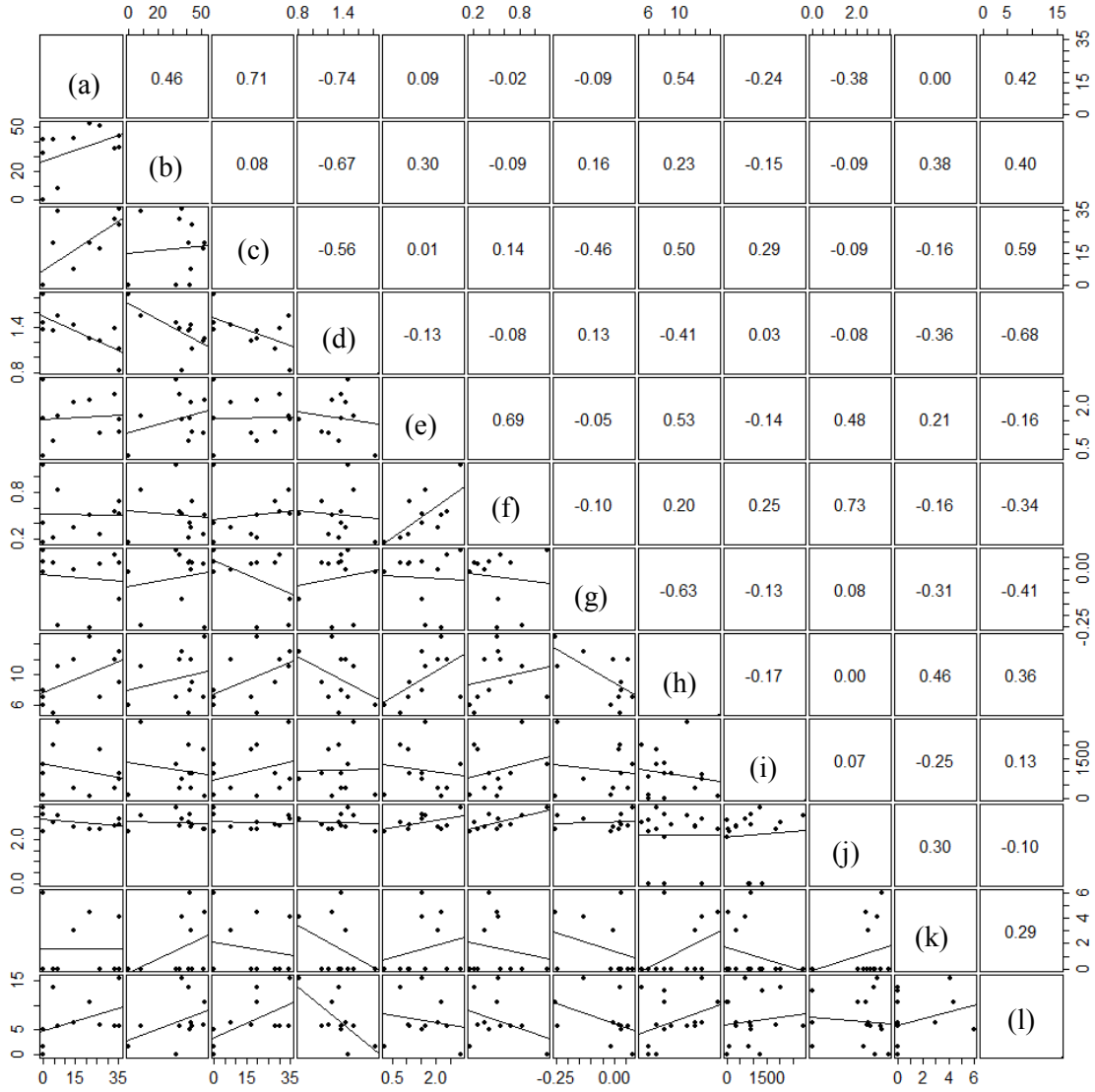

Figure C2. Scatterplot matrix of isotopic interaction metrics: (a) arcsine-square-root-transformed % isotopic overlap, (b) arcsine-square-root-transformed carbon overlap, (c) arcsine-square-root-transformed nitrogen overlap, (d) square-root-transformed distance between population centroids (DBC), (e) square-root-transformed difference in niche size (SEA_{DIFF}), (f) square-root-transformed absolute difference in trophic diversity (CD_{DIFF}), and (g) square-root-transformed difference in trophic evenness ($SDNND_{DIFF}$); and fish community variables: (h) prey species richness, (i) walleye CPUE, (j) $\log_{10}$ smallmouth bass CPUE, (k) cisco CPUE, and (l) square-root-transformed yellow perch CPUE. Correlation coefficients are reported in the corresponding box of the upper panels.

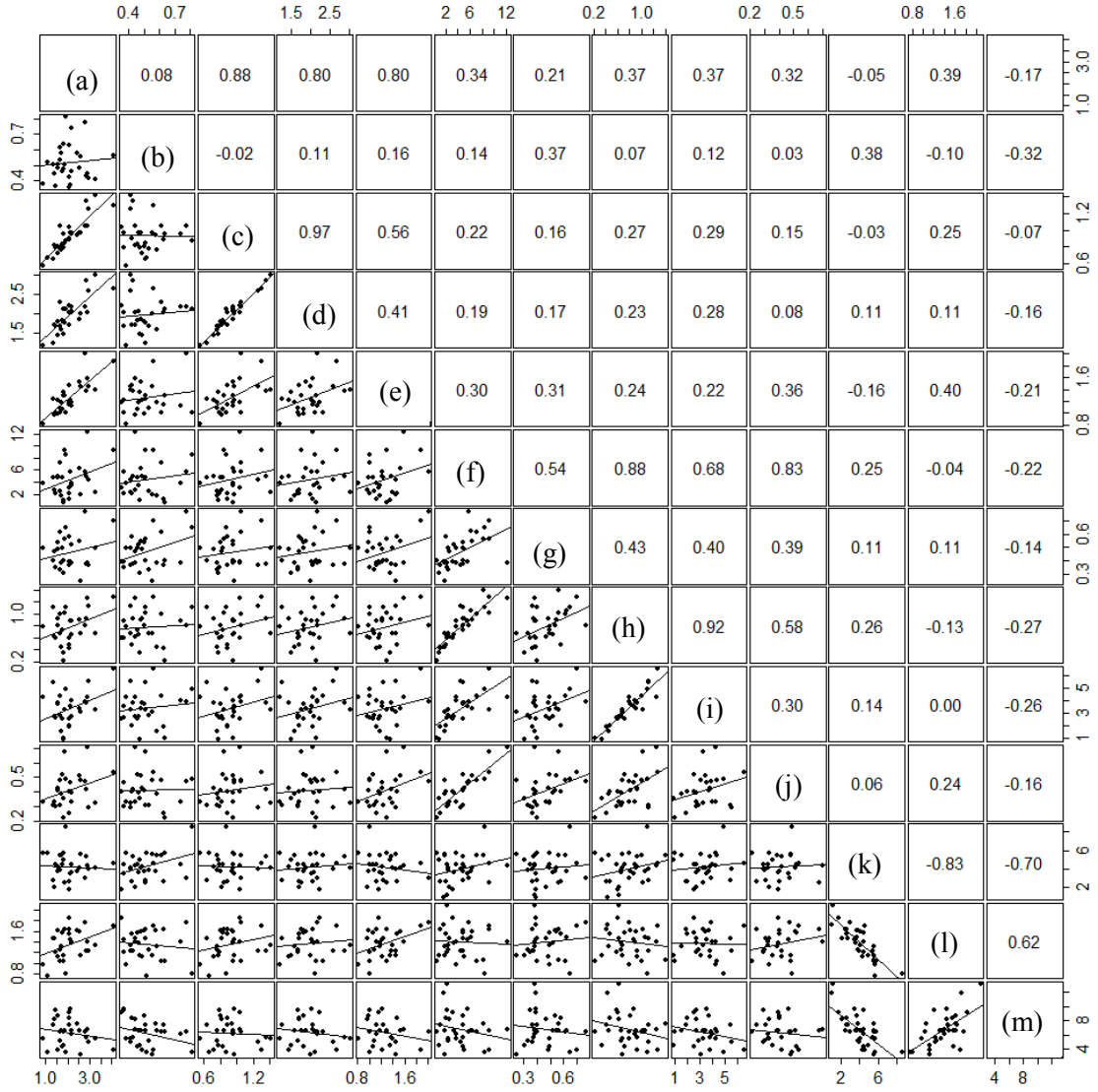

Figure C3. Scatterplot matrix of isotopic niche metrics for smallmouth bass: (a) square-root-transformed niche size (SEA_E), (b) square-root-transformed trophic evenness (SDNND), (c) square-root-transformed trophic diversity (CD), (d) square-root-transformed range along $\delta^{13}C$ axis (CR_E), and (e) square-root-transformed range along $\delta^{15}N$ axis (NR_E); isotopic niche metrics for walleye: (f) niche size (SEA_E), (g) square-root- transformed trophic evenness (SDNND), (h) trophic diversity (CD), (i) range along $\delta^{13}C$ axis (CR_E), and (j) $\log_{10}$ range along $\delta^{15}N$ axis (NR_E); and water clarity indices: (k) Secchi depth, (l) $\log_{10}$ true colour, and (m) DOC. Correlation coefficients are reported in the corresponding box of the upper panels.

APPENDIX D:

Plots of isotopic niche ellipses for all study lakes, showing trophic overlap between sympatric populations of walleye and smallmouth bass.

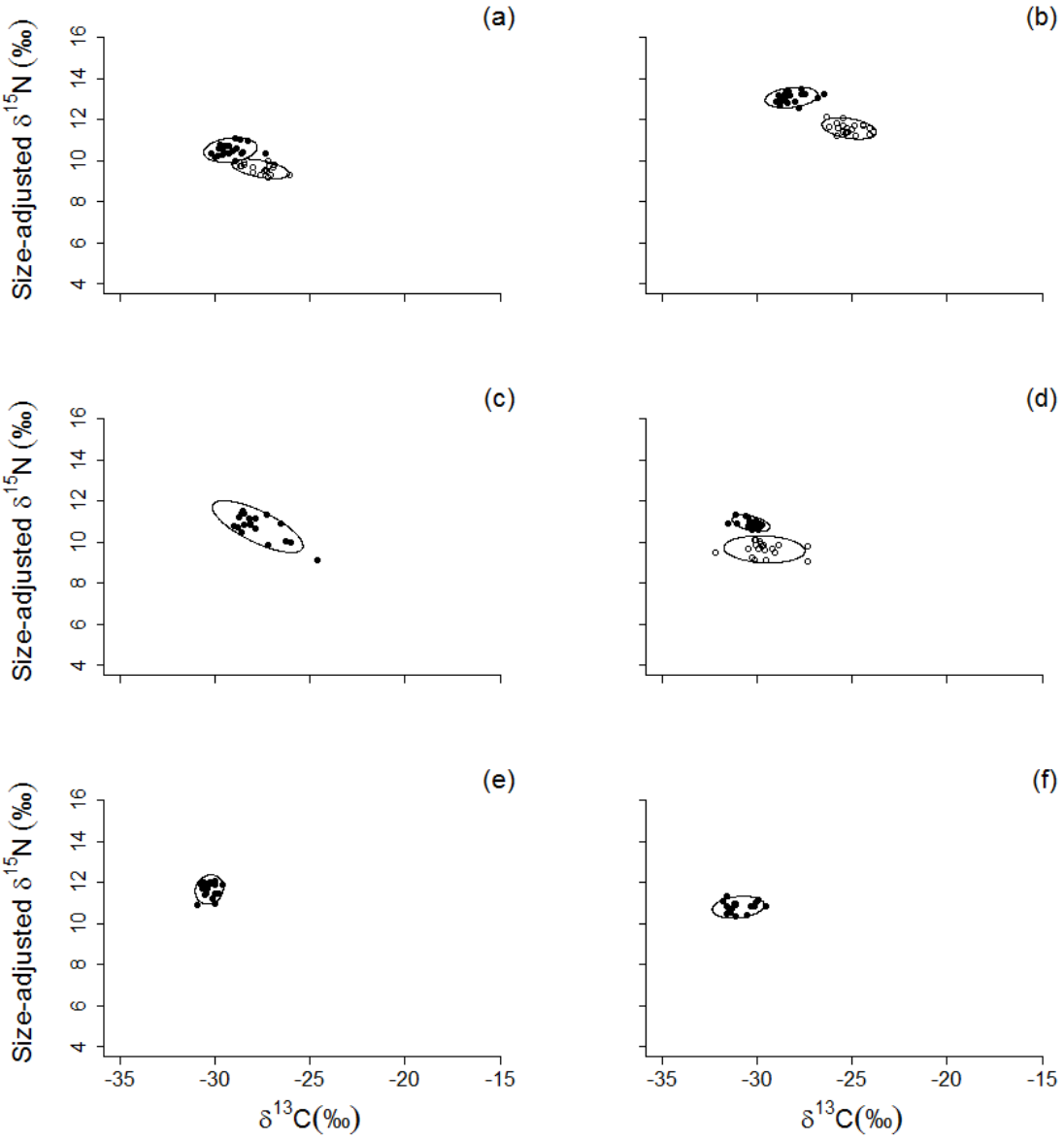

Figure D1. Plots of isotopic niche ellipses for walleye (black circles) and smallmouth bass (open circles) in (a) Addie Lake (overlap < 1%), (b) Andy Lake (overlap = 0%), (c) Augusta Lake (no smallmouth bass), (d) Bear Lake (overlap < 1%), (e) Blueberry Lake (no smallmouth bass), (f) Brandy Lake (no smallmouth bass),

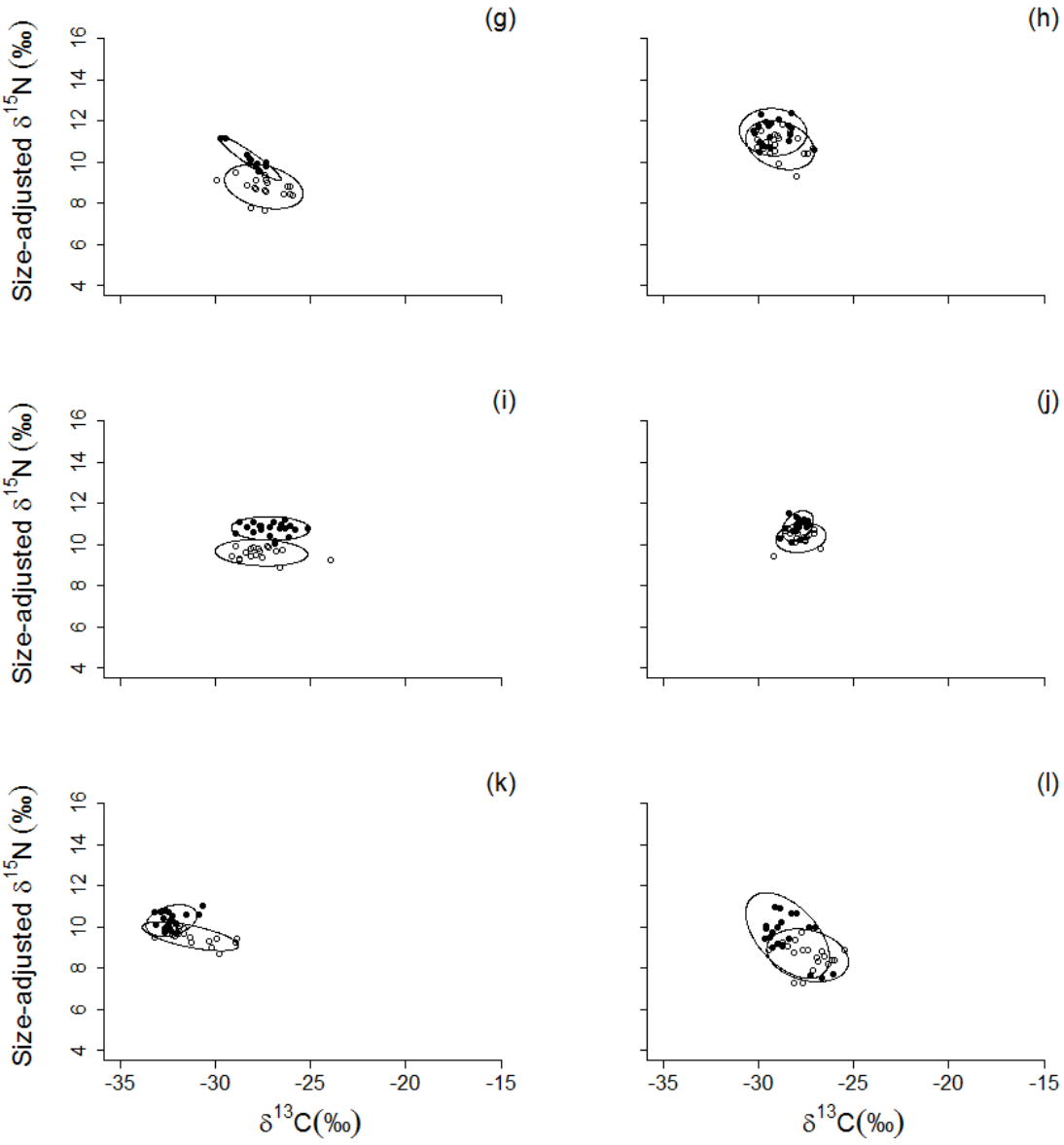

Figure D1 cont. (g) Carafel Lake (overlap = 13%), (h) Crooked Lake (overlap = 65%), (i) Cutler Lake (overlap < 1%), (j) Deerhound Lake (overlap = 43%), (k) Giroux Lake (overlap = 33%), (l) Herridge Lake (overlap = 60%),

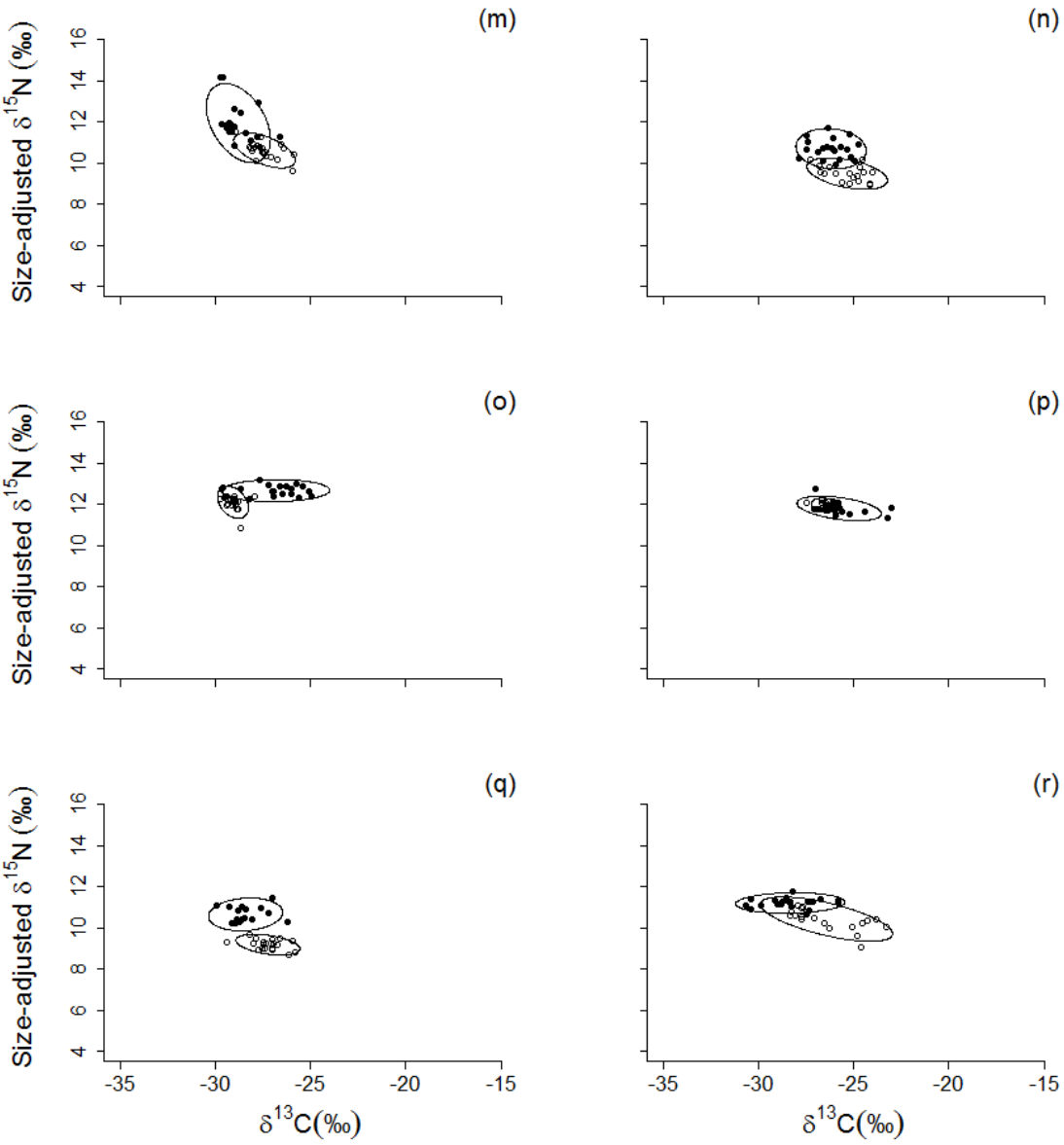

Figure D1 cont. (m) Isabella Lake (overlap = 30%), (n) Jacob Lake (overlap = 20%), (o) Kakakiwaganda lake (overlap = 15%), (p) Little Panache Lake (overlap = 35%), (q) Makami Lake (overlap < 1%), (r) Maple Lake (overlap = 36%),

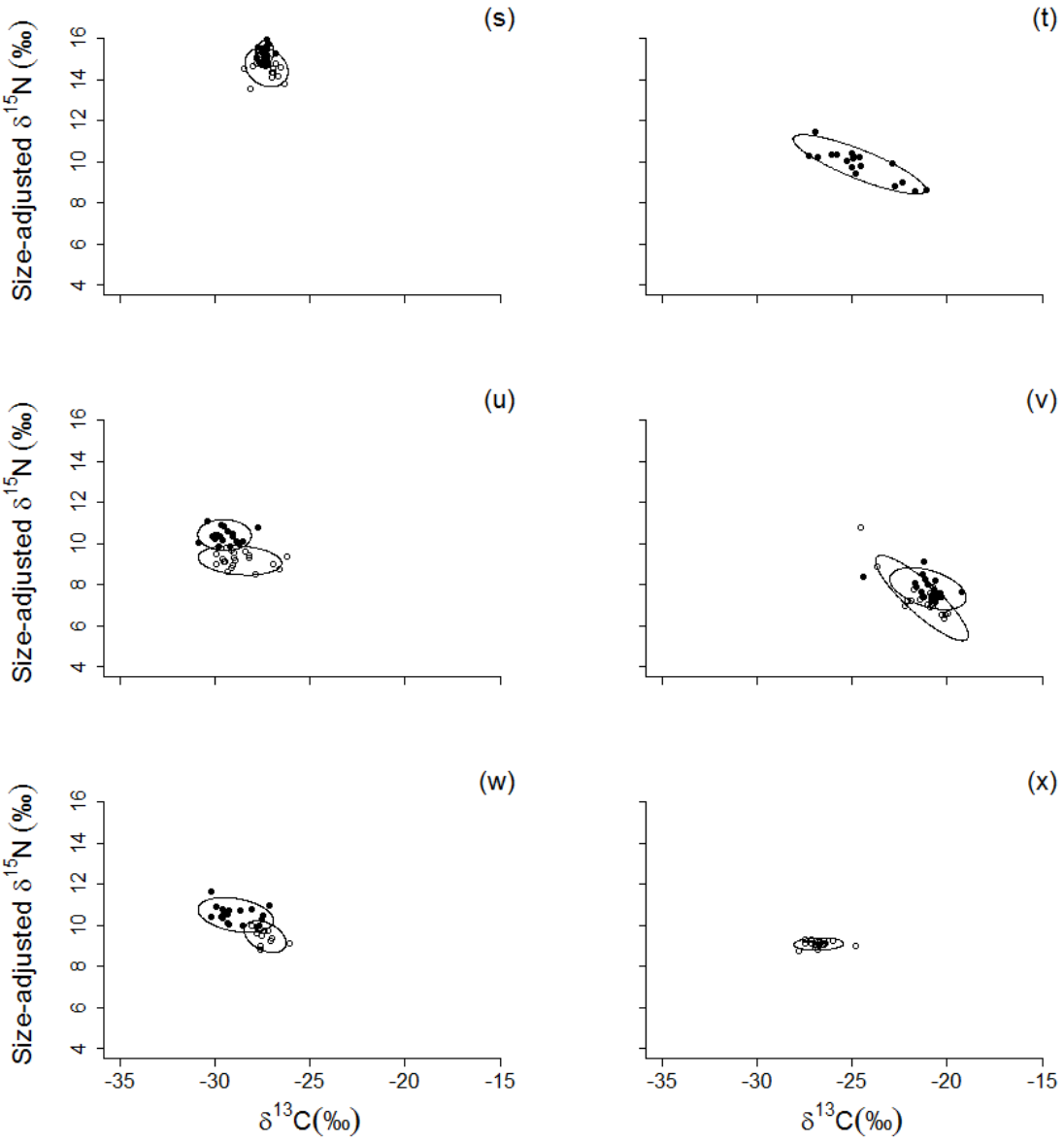

Figure D1 cont. (s) McFarlane Lake (overlap = 34%), (t) McLennan Lake (no smallmouth bass), (u) Opeechee Lake (overlap = 7%), (v) Pike Lake (overlap = 52%), (w) Pishabo Lake (overlap = 16%), (x) Rawson Lake (no walleye),

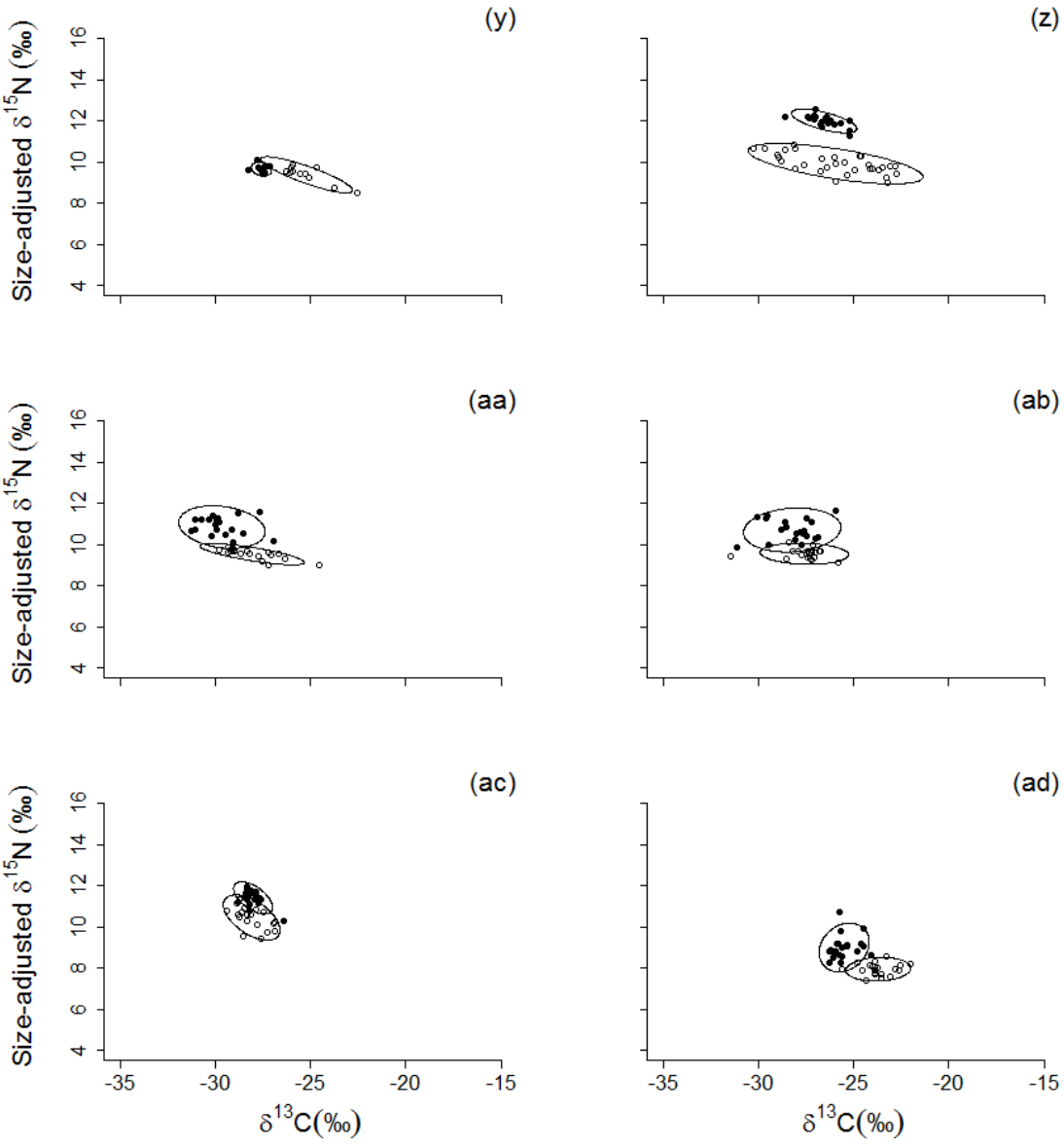

Figure D1 cont. (y) Richardson Lake (overlap = 1%), (z) Salmon Trout Lake (overlap < 0%), (aa) Shillington Lake (overlap = 6%), (ab) Shoofly Lake (overlap = 15%), (ac) Smith Lake (overlap = 24%), (ad) St. Leonard Lake (overlap = 4%),

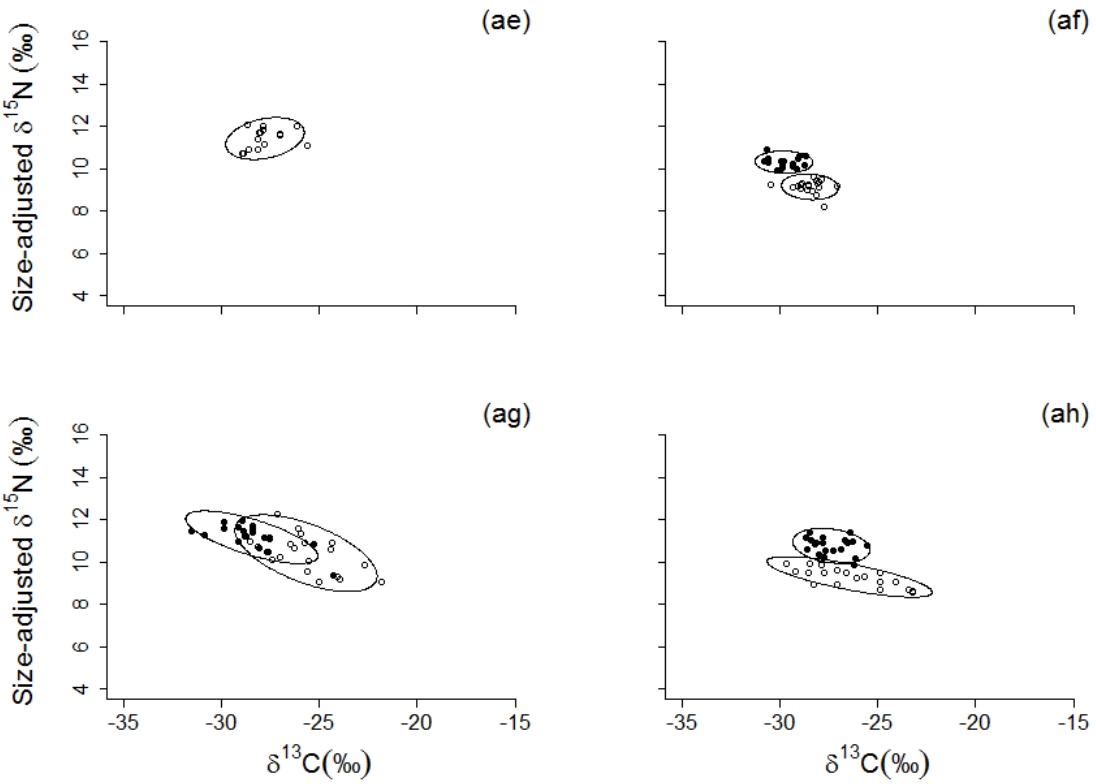

Figure D1 cont. (ae) Stewart Lake (no walleye), (af) Thieving Bear Lake (overlap < 1%), (ag) Twin Lake (overlap = 44%), (ah) Wilson Lake (overlap = 2%).